Fossil Mammals of Africa

No. 10

FOSSIL TUBULIDENTATA
FROM EAST AFRICA

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With 4 plates and 13 figures in the text

FOSSIL MAMMALS OF AFRICA

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FOSSIL TUBULIDENTATA FROM EAST AFRICA

By D. G. MacInnes

INTRODUCTION

The fossils described in this paper were found on Rusinga and Mfwangano Islands, Victoria Nyanza, during the seasons 1948–1952; the majority being discovered in June 1950.

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Order TUBULIDENTATA

Family ORYCTEROPODIDAE

MYORYCTEROPUS gen. nov.

DIAGNOSIS.—A genus of Tubulidentata in which the angle between the horizontal mandibular ramus and the anterior border of the ascending ramus is about 45°. Upper M^3 distinctly bi-lobed.

Myorycteropus africanus sp. nov.
(Plates 1, 2; Text-figs. 1–10)

DIAGNOSIS.—A species of *Myorycteropus* with the dental formula $\frac{?.\ ?.\ 4\text{--}5+.\ 3}{?.\ ?.\ 4+.\ 3}$. Upper M^3 distinctly bi-lobed. Size between 50% and 60% that of *Orycteropus afer lademanni* Grote. Humerus with breadth of distal end equal to $\pm48\%$ of total length. Femur with third trochanter crest occupying $\pm22 \cdot 5\%$ of total length.

HOLOTYPE.—Parts of skull, mandible and associated skeleton No. 1264 '50 from Rusinga Island.

HORIZON.—Lower Miocene (*see* Le Gros Clark & Leakey, 1951).

LOCALITY.—Rusinga Island (R.2–4 series, Kulu-Waregi), Victoria Nyanza, Kenya Colony, Lat. 0° 25′ S.: Long. 34° 11′ E.

MATERIAL.—The holotype, comprising part of the skull and mandible, with most of the upper and lower teeth (Pl. 1, figs. 1–4). A few fragments of the axial skeleton and ribs. Parts of both scapulae; the right clavicle; both humeri, radii and ulnae; right trapezium, and various metacarpals and phalanges. Parts of the pelvic girdle; both femora, tibiae and fibulae; most of the left tarsus, and a few posterior phalanges.

In addition to the holotype, a fragment of the right mandibular ramus from Kiahera Hill, Rusinga (No. 23 ’48), containing the alveolar ends of five teeth (Pl. 1, fig. 8); two small fragments of a right and a left mandibular ramus, each bearing M_3, were recovered from the neighbouring Mfwangano Island (Nos. MW. ’50 & MW. 61 ’52 respectively), and a left astragalus from the R.1 series of Rusinga.

DESCRIPTION.—The holotype is a sub-adult animal, as shown by the imperfectly fused epiphyses of some of the limb bones. In most cases, however, they are very closely united, and in some completely fused. A specimen of the modern *Orycteropus afer* in approximately the same stage of development was examined, and it was found that there was virtually no difference in size from that of a fully adult animal. Thus it may be assumed that although the fossil was not quite fully mature, it had probably attained its full size. On the basis of the limb-bones this appears to have been little more than 50% of the size of *Orycteropus afer lademanni*, the Recent representative of the group in the same area. A typical adult skeleton of this sub-species has been used throughout as a basis for comparison.

SKULL.—Only a small part of the left maxilla is preserved (Pl. 1, figs. 1–2) and it is thus impossible to obtain a very clear idea of the general outline of the skull. It appears, however, to have been relatively lower than that of the modern animal. The infra-orbital foramen is very large, and although situated at about the same relative height above the alveolus, it appears to be very nearly in the middle of the total vertical height of the skull, whereas in *Orycteropus* its height above the alveolus is only about one-quarter of the total height of the skull at this point.

Colbert (1941) suggested that the position of the infra-orbital foramen in its relation to the dentition may vary in the Recent genus, on account of the tendency for the tooth-row to move forwards as the age of the animal increases. On the other hand he suggested that there is a constant and significant difference between the Upper Pliocene *O. gaudryi* and the Recent species in the position of the anterior margin of the orbit in relation to the dentition. In the former it is always over the second molar, and in the latter always over the third molar. This would imply that he considers the relative position of M^3 to remain the same, and thus, that any forward movement of the tooth-row is brought about by a gradual lengthening of the distance between the anterior tooth and the third molar, since if the whole tooth-row were to move forward, including M^3, the relative position of the orbit would surely be as variable as that of the infra-orbital foramen. Assuming that the relationship of orbit to M^3 is significant, it is found that in a series of skulls of *O. afer lademanni*, taking the tooth-row as the horizontal, the average distance between perpendiculars through the posterior border of the infra-orbital foramen and the anterior rim of the orbit is 19 mm. Similarly the average distance between perpendiculars through the posterior border of the infra-orbital foramen and that of M^3, is 29 mm. The ratio

of these measurements is found to be virtually identical in Colbert's figures of *O. gaudryi*.

In the fossil under consideration no part of the orbital rim is preserved, but the horizontal distance from the infra-orbital foramen to the posterior wall of M^3 is 12 mm. Thus, if the proportion were approximately similar, the anterior edge of the orbit should have been about 8 mm. behind the infra-orbital foramen, or immediately over the space between the second and third upper molars. However, it is also clear from Colbert's figures that the proportions of these measurements are somewhat different in the case of the Recent West African species *O. erikssoni*, as they are in the Pleistocene species described below, and it would therefore be unwise to attach undue importance to a character of such doubtful value.

For convenience, the sequence in the cheek teeth is here regarded as the normal unspecialized arrangement of four premolars and three molars; any teeth anterior to the first premolar being regarded as additional anterior premolars.

Five teeth are in place in the maxillary fragment, including the three bi-lobed molars and the last two premolars, but the specimen is broken immediately in front of the anterior tooth (Pm^3). In addition, a single tooth, which appears to be a left upper premolar, was found in the matrix surrounding the skeleton. A small part of the bone is attached, in which the inner surface of the socket for another posterior tooth is clearly visible. This does not fit the anterior tooth in the maxillary fragment, and it thus seems probable that the tooth is Pm^1, with part of the socket for Pm^2.

In the specimens of *O. afer* available for comparison, the length of the upper tooth-row is found to be 96% of the lower. In the case of the fossil, the lower tooth-row measures 46·5 mm., and the length of the upper tooth-row is therefore estimated as about 44·5 mm., or 12·5 mm. more than is actually preserved in the maxilla fragment. This would probably have accommodated three anterior teeth, namely one additional premolar besides Pm^1 and Pm^2.

Upper Dentition.—A very minute isolated tooth was found in the matrix around the skeleton. It is oval in section, measuring $2 \times 1·25$ mm., and is probably an additional left upper premolar, but its exact position is not known.

In cross-section Pm^1 is a compressed oval, and the shaft has a marked backward curvature of the root portion. The occlusal surface is divided by a sharp antero-internal–postero-external ridge, separating two sub-equal planes of wear. The two posterior premolars are bilaterally compressed, particularly Pm^3, in which the maximum width is slightly less than half the maximum length. In this tooth there is a slight constriction on either side, so that the maximum width is across the anterior half, while the median width is about 0·3 mm. less. In Pm^4 the median lateral constriction is not apparent. The molars, including M^3, consist of two lobes separated by a deep vertical groove in the middle of both the lingual and the labial surfaces. In M^3 the posterior lobe is somewhat truncated in its outer part, but the transverse section is entirely different from that of *Orycteropus*, in which the third molar is normally a simple oval with, at most, only a very faint trace of the vertical groove.

A characteristic feature of these teeth is that the internal dentinal columns are clearly visible both in the crown and at the sides, and there is no visible external cementum. This feature can be seen in Pl. **1**, fig. 6, which is an untouched photograph. In modern teeth of *O. afer* the dentinal columns are very indistinct except

near the root, until a section is cut, but it is possible that post-mortem weather action, prior to the embedding of the specimen in the deposit, might have removed a surface layer of cementum from the sides of the teeth. On the other hand, the fact that so much of the skeleton was preserved with the component parts at least in close association, though not articulated, suggests that the body must have become sealed in the deposit before decomposition was far advanced. In addition to the teeth in the left maxilla fragment, an isolated Pm^4 and M^1 from the right side were found in the surrounding matrix.

The measurements of the upper teeth, in millimetres, are as follows:

	Maximum Length	Breadth anterior lobe	Median con- striction	Breadth posterior lobe	Index
Left					
Pm^1 . .	3·25	1·75	—	—	54
Pm^3 . .	5·20	2·50	—	—	48
Pm^4 . .	5·50	3·00	—	—	54
M^1 . .	7·20	4·70	2·70	4·50	65
M^2 . .	6·25	5·10	3·50	4·80	81
M^3 . .	4·75	5·00	3·50	3·80	105
M^1–M^3 . .	19·25	—	—	—	—
Pm^3–M^3 . .	32·25	—	—	—	—
Right					
Pm^4 . .	5·30	3·00	—	—	57
M^1 . .	7·10	4·80	3·00	4·75	68

An isolated premolar (No. 369 '52) recovered from the Kathwanga deposits of Rusinga Island in 1952 is provisionally referred to the new genus. The tooth appears to be a left upper Pm^4, but the shape and the attrition surfaces are unlike those of Pm^4 of the holotype, and also unlike any example of *O. afer* available for comparison. The transverse section is oval, with the greatest diameter in the anterior part. Assuming that the tooth is correctly determined as the left upper Pm^4, the highest point of the crown is antero-external, with the large concave facet worn by contact with the lower Pm_4 occupying fully three-quarters of the occlusal area. A small facet along the postero-external border represents wear against the lower M_1. In all the specimens of *O. afer* examined, and also in the holotype of *Myorycteropus*, more than half of the crown is occupied by the M_1 facet, and the crest separating the two worn surfaces is approximately at right angles to the long axis of the tooth, whereas in the tooth under consideration the crest is diagonal. In length this upper Pm^4 corresponds exactly with those of the holotype, but in breadth it is intermediate between the latter and those of the recent genus. The comparative measurements, in millimetres, are as follows :

	Myorycteropus holotype	Kathwanga specimen	*Orycteropus afer*
Pm^4 :			
Length . .	5·50	5·50	7·40
Breadth . .	3·00	4·00	5·60

MANDIBLE.—A large part of the left half of the mandible is preserved, including most of the tooth-row, but the anterior part is missing (Pl. 1, figs. 3, 4, and Text-fig. 1). Part of the right side is also preserved, but is much more severely affected by weathering. The most conspicuous feature is the shallow angle between the body and the ascending ramus. Taking the general line of the gingival level from the anterior tooth to M_3 as the base-line, the angle formed by the anterior border of the ascending ramus is approximately 45° (Text-fig. 1a). In *O. afer lademanni* this angle is normally about 70°, and Colbert's figure of the mandible of *O. erikssoni* also shows an angle of approximately 70°, whilst that of *O. gaudryi* has an angle of nearly 80°. Colbert (1941) suggested that the Recent species may have developed from the Pliocene form *O. gaudryi* by a gradual lengthening of the skull and mandible, and if
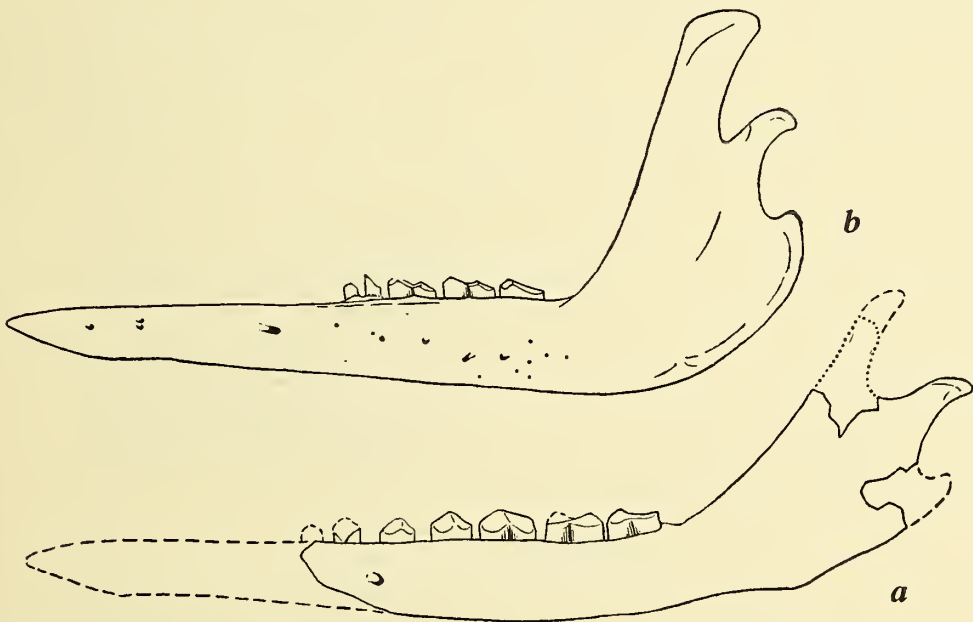

FIG. 1. (*a*) *Myorycteropus africanus*. Left mandibular ramus. ×⅟₁. (*b*) *Orycteropus afer*. Left mandibular ramus. ×½.

this is correct, the more upright angle of *O. gaudryi* is what would naturally be expected. On the other hand, in the much earlier Lower Miocene fossil the attenuation is relatively greater even than that of the Recent species. This suggests either that the Miocene genus is not in the direct ancestral line of the existing group, or that *O. gaudryi* is, in fact, more specialized than the Recent species, and not more primitive.

In the immature stages of many mammals the angle between the body and the ascending ramus of the mandible is more shallow than in the adult, and the fact that the holotype of *Myorycteropus* is not fully mature must be taken into consideration when discussing this point. On the other hand, for reasons already mentioned, the animal in question is thought to have attained its full size. Moreover it is unlikely

that the general shape of the mandible would be effectively modified after the third lower molar had erupted and become functional.

The effect of the shallow mandibular angle is to bring the condyle relatively further back, so that it becomes the most posterior point of the mandible, whereas in *Orycteropus* the most posterior point is generally the angle, which may project up to seven millimetres behind the level of the condyle. The extreme posterior part of the angle is missing in the fossil, but it certainly cannot have extended behind the level of the condyle. The upward projection of the coronoid process is also missing, but since there appears to be no distortion it is possible to reconstruct the hind end of the mandible with some degree of accuracy. Unfortunately the slender anterior part of the mandible is not preserved, and it is thus impossible to determine the exact degree of attenuation that existed.

In a series of Recent mandibles, the average distance from the posterior border of M_3 to the anterior tip of the horizontal ramus is 139 mm., of which the three molars occupy 39·5 mm., or 28·5%. The part anterior to the molars measures 99·5 mm., or 71·5%. Taking the same proportions for the fossil, the portion anterior to the molars should have measured 59 mm., of which only 23 mm. is preserved. Thus it is probable that about 36 mm. of the anterior part is missing, and the original total length of the mandible is therefore estimated as 123 mm.

Parts of seven teeth are present, but although the specimen is broken at the level of the anterior tooth, it is unlikely that any teeth have been lost. The space occupied by the lower cheek teeth is 46·5 mm. long.

The wear in the lower teeth is very oblique, so that M_1 projects 4 mm. above the alveolus on the lingual side, and only 1·75 mm. on the labial side. This is not noticeably reflected in the upper molars, in which the wear on the lingual side is not appreciably greater than on the labial. On the other hand the wear on the upper premolars is distinctly oblique, which implies that the lower tooth-rows converged somewhat more sharply than the upper.

In *Orycteropus* there are generally several minor foramina on the outer wall of the ramus below the teeth, but the main mental foramen is situated well forward, from 16 mm. to as much as 33 mm. in front of the anterior tooth. In the fossil, the mental foramen is situated below the anterior border of Pm_3, and is thus at least 11 mm. behind the level of the anterior tooth. In addition, a single, very minute subsidiary foramen is present below Pm_4. A second mandibular fragment (No. 23 '48) from site R. 113, Kiahera, has two sub-equal foramina, one situated below Pm_2 and the other below the anterior border of Pm_4.

The skull and mandible of a sub-adult example of *O. afer lademanni* at approximately the same stage of development (Coryndon Museum collection) has six teeth in the lower jaw, of which the anterior is vestigial, and is separated from the other teeth by a diastema of 16 mm. In the fossil all seven teeth are virtually in closed series, and the anterior premolar (Pm_1) is not only relatively but actually larger than the anterior tooth (Pm_2) of the Recent animal.

LOWER DENTITION.—The crown of Pm_1 is missing, but the root remains in the alveolus. This shows a laterally compressed cross-section, and the socket is set somewhat obliquely, indicating that the crown projected slightly forwards. Pm_2 has also lost most of the crown, but again the cross-section is a compressed oval. Pm_3

is nearly complete, and, although slightly damaged on top, it appears to have been worn to a point by contact between the second and third upper premolars. The cross-section is oval, and there is no trace of the median vertical groove on either side in any of the first three premolars. Pm_4 is relatively broader than any of the preceding teeth, and has a shallow vertical groove on the labial wall, whilst the lingual surface is convex and has no trace of a groove. The worn surface is sharply oblique towards the outside, making an angle of about 43° to the general vertical axis of the ramus. M_1 is a typical bi-lobed tooth, with a deep median vertical groove on either side. The posterior lobe is slightly broader than the anterior, and the wear is again sharply oblique. In M_2 the lateral grooves are deeper, and the posterior lobe is the broader. The wear appears to be rather less oblique, but since the lingual side of the crown is somewhat damaged it is not possible to determine the angle of wear accurately. M_3 is bi-lobed, with the greatest width across the anterior lobe. The lateral grooves are very much more pronounced than is usual in the corresponding tooth of *Orycteropus*.

The measurements of the mandible and lower dentition of the holotype, in millimetres, are as follows:

Maximum length of specimen . . .	87·0
Estimated original length	123·0
Depth of ramus at Pm_1	10·3
Thickness of ramus at Pm_1 . . .	3·0
Depth of ramus at M_3	11·0
Thickness of ramus at M_3 . . .	7·0
Length of premolar series	22·2
Length of molar series	23·2
Length Pm_1–M_3 inclusive	46·0

	Maximum Length		Breadth at						Index	
			Anterior Lobe		Constriction		Posterior Lobe			
	Lt.	Rt.	Lt.	Rt.	Lt.	Rt.	Lt.	Rt.	Lt.	Rt.
Pm_1 . .	2·50	—	1·30	—	—	—	—	—	52	—
Pm_2 . .	4·20	—	2·00	—	—	—	—	—	48	—
Pm_3 . .	4·80	4·60	2·30	2·50	—	—	—	—	48	54
Pm_4 . .	5·50	5·40	2·75	3·00	—	—	—	—	50	55
M_1 . .	7·70	7·50	3·50	3·40	2·50	2·50	4·00	4·00	52	53
M_2 . .	8·00	7·90	4·00	4·10	2·60	2·75	4·75	4·75	59	60
M_3 . .	6·30	6·50	4·50	4·75	3·00	3·00	3·75	4·00	71	73
Pm_1–M_3 .	46·00	—								
M_1–M_3 .	23·20	22·50								

$$\text{Index} = \frac{\text{Maximum breadth} \times 100}{\text{Length}}.$$ In M_1–M_2 the maximum breadth is at the posterior lobe.

In addition to the holotype, three small fragments of mandibles have been found. One of these, from Kiahera Hill, Rusinga (No. 23 '48), comprises part of the right horizontal ramus containing the roots of four premolars and the anterior end of the first molar. Since the specimen was of little value in itself, the upper edge was ground down to about 1 mm. below the gingival level and polished to expose the internal structure of the roots. Part of this ground section is shown in Pl. 1, fig. 8. The measurements of these teeth, in millimetres, taken at the gingival level prior to sectioning, are as follows:

	Pm_1	Pm_2	Pm_3	Pm_4
Length . .	2·40	3·30	4·20	5·40
Breadth . .	1·60	2·00	2·50	2·75

Two other examples were found on Mfwangano Island; MW. '50 being from the right side and MW. 61 '52 from the left. Each includes the lower M_3 and part of the empty socket for M_2. The bone of the ramus is more massive than in the holotype, but the transverse section is almost identical in shape except that there is a marked lateral constriction at the level of the third molar, whereas in the holotype the constriction is more posterior.

The third molars are relatively broader in the anterior lobe, although approximately similar in length to those of the holotype. The measurements of these examples, in millimetres, compared with similar measurements of the left ramus of the holotype, are as follows:

	23 '48 Rt.	MW. '50 Rt.	MW. 61 '52 Lt.	Holotype, Lt.
Depth of ramus at Pm_4 .	10·00	—	—	10·60
Depth ,, ,, ,, M_3 .	—	14·40	13·50	11·00
Thickness ,, ,, Pm_4 .	6·50	—	—	5·00
Thickness ,, ,, M_2 .	—	10·00	9·50	6·75
Thickness ,, ,, M_3 .	—	7·75	7·75	7·00
Length of M_3 . . .	—	6·10	6·75	6·30
Breadth of M_3 at anterior lobe	—	5·60	5·50	4·50
,, ,, ,, at constriction	—	3·50	3·00	3·00
,, ,, ,, at posterior lobe	—	3·80	3·80	3·75

Tooth structure

The name Tubulidentata was applied to this group of mammals on account of the structure of their dentine. In consequence, the term "tubule" has been widely used for the conspicuous dentinal columns of which the teeth are composed. In dental anatomy the term "tubule" is applied to the very fine canals which permeate mammalian dentine from the pulp, and which enclose the "Tomes" fibres. Each of the vertical columns in a tooth of *Orycteropus* comprises a central column of pulp, enclosed by dentine which is itself penetrated by innumerable "tubules" (Pl. 4, fig. 6). For this reason the terms "column" or "pillar" are here used to denote the relatively large vertical components which enclose the pulp canals, while "tubules" denotes the much smaller channels radiating within the dentine from the central pulp.

The internal tooth-structure was exposed in the holotype by fractures of the left upper Pm^4 (Pl. 1, fig. 5) and the left lower M_2 (Pl. 1, fig. 7). This revealed a condition

somewhat similar to that described originally by Oldfield Thomas (1889–90) in the milk dentition, and later by Anthony (1934) in the "young" or undeveloped tooth of *Orycteropus*. It consists of irregular rounded columns set in a homogeneous matrix. Transverse sections of every tooth not associated with the holotype skeleton showed the normal adult condition with the honey-comb pattern of contiguous polygonal columns (Pl. 1, fig. 8). This supported the view that the holotype was not fully mature, and in order to obtain further information about the change of structure, the detached upper Pm^4 and M^1 of the right side were polished at both ends to determine whether any marked development was apparent within the length of a single tooth. These sections (Pl. 2, figs. 1, 3) reveal that the concentration of columns is somewhat greater at the apex than at the crown, and it seems therefore that in the early stages the teeth develop by an increase in the number as well as in the size of the individual columns, and at the same time the matrix is proportionately reduced.

Transverse sections made near the apex in Recent *Orycteropus* teeth show that in the early stages the inter-columnar matrix is not only continuous with the external cementum, but it contains cementoblasts and indeed seems to represent normal cementum. The continuity of the external cementum with the inter-columnar matrix is also evident in the transverse section of a tooth of the Pleistocene species described below (Pl. 4, fig. 7). Proceeding towards the crown the columns become closely adjacent, but are always separated from one another by more or less distinct lines (Pl. 4, fig. 6). Occasionally three or more adjacent columns do not quite meet in a point, but enclose a relic of the inter-columnar matrix in which cementoblasts may sometimes be seen. It is assumed, therefore, that the lines separating the contiguous columns are composed of cementum. This agrees with Owen's statement (1840–45) that the individual "denticles" are bound together by cement, although Duvernoy (1853) and later Anthony (1934) regarded the matrix as a form of dentine. In the tightly compact honey-comb pattern the intervening lines of cementum are discontinuous, and with certain stains appear as dotted lines (Pl. 4, fig. 6). Under high magnification dentinal tubules may be seen passing between the islands of cementum, and connecting the dentine of adjacent columns. This is perhaps what is meant by Heuvelmans (1939) when he refers to the lines as being composed of a mixture of ivory and cementum. In the fossil, no tubules have been seen penetrating the matrix, which is therefore regarded as plain cementum.

Pm^4 of the left side shows what appears to be the earliest stage of development, in which the dentine columns are extremely variable in size and irregular in distribution; they are also relatively larger than those in the teeth of more recent forms. A transverse section at about 2 mm. below the occlusal surface shows that at this stage the columns of the periphery are small and closely adjacent, and form a well-defined peripheral band about 0·25 mm. in breadth. The columns of the main body of the tooth, however, are larger and isolated, or in clusters of two or three, separated from one another and therefore with rounded outlines, but bound together by the cementum.

Under a high magnification each column shows an opaque central spot surrounded by a homogeneous translucent area, and an outer semi-translucent border in which the radiating dentinal tubules are visible. It is probable that the whole of the translucent central portion of each column represents a calcite in-filling of a large pulp

canal such as would be expected in a tooth in the early stages of its development. The cementum, or inter-columnar matrix, has no translucence, but seems to have a somewhat granular texture, which produces an appearance of "flow-structure" between the columns of dentine.

Pm^4 of the right side was sectioned at both ends, and although the coronal section (Pl. **2**, fig. 1) is mainly similar to that already described, it is slightly further developed, since the peripheral band of contiguous columns is 0·5 mm. in breadth, and it is less clearly defined. The section at the root of the same tooth (Pl. **2**, fig. 3) shows that the peripheral band now measures 1·0–1·5 mm. in breadth, and thus occupies by far the greater part of the total area, while the few remaining isolated columns have already become somewhat angular in outline.

A further stage in the development of the columns is shown by the first upper molar of the right side. The inter-columnar cementum is reduced to give the characteristic linear pattern, and all the columns have become polygonal. It is probable that M^1 is the first of the permanent teeth to come into wear, and this may account for the fact that the tooth shows a more advanced stage of development than Pm^4, but on the other hand the first molar of the left side appears to have rounded central columns and a distinct peripheral band, and the degree of development may thus be variable.

In the right Pm^4 the number of columns per square millimetre at the occlusal level, in ten random counts, varied from 11 to 18, with an average of 14·4. At the root level it varied from 14 to 23, with an average of 19·5. Thus it seems that the number of columns increases throughout the early development until the characteristic adult condition of contiguous polygonal pillars is achieved.

A fracture of part of the crown of the second lower molar reveals that the columns of the central part of the tooth are more compact and regular than those of the upper premolar, but they are again rounded in cross-section, and set in an inter-columnar cementum. The peripheral band is even more marked than in the premolar, and its columns appear to be separated from the central area by a continuous narrow layer of cementum. Those of the periphery tend to be slightly elongated along the radial axis, and in this respect bear a superficial similarity to the condition observed by Lönnberg (1906) in a "supernumerary" (additional anterior Pm) tooth of *O. capensis*, but in the latter there is no clear-cut differentiation between these columns and the rest of the tooth.

The fragment from Kiahera Hill (23 '48) has the roots of four premolars and part of the anterior lobe of the first molar. Since no crowns were preserved the fragment was ground and polished to a depth of about 1 mm. below the gingival level, and in transverse section the columns are polygonal throughout. Similarly in two of the other three teeth preserved, the honey-comb pattern is distinct, while in the remaining tooth, which was not sectioned, the typical columnar structure is visible where the lower end is exposed. The Kiahera fragment is naturally stained, perhaps by manganese; consequently the in-filling of the central pulp canals and much of the inter-columnar cementum in part of the first molar is black and very distinct. In the fourth premolar the stain is less intense and the pattern is very indistinct, but the average of five counts in each tooth gave a concentration of 16 columns per square millimetre in the premolar, and 19 in the molar.

Several teeth of *O. afer* were sectioned for comparison with the fossil material, and it was found that the bulk of the columns were normal although variable in size in different teeth. In one example of a fourth upper premolar the columns of the outer part are normal, whereas those of the central portion are very irregular, in some cases merging together to form a most complex pattern (Pl. 4, fig. 1). There is a slight superficial similarity in this structure to that of the upper premolars of *Myorycteropus*, but there is no trace of the inter-columnar matrix except in the well-defined lines separating the individual groups of columns. This irregularity appears to be abnormal, since no other tooth shows a comparable arrangement, and even the opposite tooth of the same skull has the normal structure.

In *O. afer lademanni* the great majority of the columns are sub-equal in size, but occasional larger or smaller pillars occur throughout the tooth. In the specimens examined the range of variation was found to be from 0·1 mm. to 0·4 mm. in diameter, with the average about 0·2 mm. The range of variation in the columns of *Myorycteropus* is almost similar; from 0·125 mm. to 0·5 mm. Thus, although the animal was considerably smaller, the dentine columns are in some cases larger than those of the Recent species.

According to Colbert (1933) the columns in *O. gaudryi* are more or less evenly graduated in size, with the larger at the periphery, whereas in *O. browni* from the Middle Siwaliks, both large and small columns occur throughout the tooth. In *O. afer* there is a slight gradation, as in *O. gaudryi*, from the larger columns near the outside to smaller pillars near the centre of the tooth. This is best shown by the photomicrograph, Pl. 4, fig. 5, which represents part of the transverse section of the anterior lobe of a lower M_2 of *O. afer*. The specimen was stained with iodine to pick out the details of structure, and the reproduction is approximately ×25 diameters. The gradation in size is somewhat exaggerated by the fact that the more densely stained areas immediately surrounding the pulp canals are larger in the middle of the tooth, but it was found that the average of a number of counts gave a concentration of 30 columns to the square millimetre in the middle, and 25 in the outer part.

On the other hand there is no doubt that the individual columns increase in size in proportion to the age of the animal. Thus a section through the tooth of a very aged individual (Pl. 4, fig. 2) gave concentrations varying from only 9 to 16 per square millimetre.

Jepsen (1932) pointed out that in the teeth of *Orycteropus* many of the columns arise from the outside, and a longitudinal section through a molar of *O. afer* confirms this (Pl. 4, fig. 3). Moreover the lateral view of any Recent Ant-bear tooth from which the cementum has been removed shows the exposed openings of several canals, which are directed inwards and upwards towards the crown. A similar condition is found in *Myorycteropus*, and a longitudinal section of the right upper Pm^4 (Pl. 2, fig. 2) shows that while the central columns appear to be mainly parallel, some of those at the sides converge inwards as they pass up towards the crown.

POST-CRANIAL SKELETON.—Very few bones of the axial skeleton are preserved. These include the first cervical vertebra; parts of five thoracic vertebrae, possibly Nos. 5–9, and three caudal vertebrae.

The atlas vertebra is practically complete and very well preserved (Text-fig. 2a).

The superior arch is very broad antero-posteriorly, with a small spinous process; it is penetrated by an enclosed foramen for the passage of the first cervical nerve. On the dorsal surface of the arch the nerve channel is visible as a deep open groove, but whereas in *Orycteropus* this remains open until it unites with the vertebrarterial canal, in the fossil it penetrates an extension of the transverse process, emerging again on the lower surface of the process in the anterior, or lateral aperture of the foramen transversarium (Text-fig. 2). Internally the main aperture for the spinal cord is more rounded in the fossil, lacking the median lateral constriction of the Recent animal owing to the less prominent inner flanges of the posterior zygapophyses. The inferior arch is very slender, and almost cylindrical in section.

In the thoracic vertebrae most of the epiphyses and processes are lost, but in four specimens the neural arch is complete, one example having the whole of the neural spine, and another one of the transverse processes. The laminae of the arch are flattened dorso-ventrally as in the Recent species, and produced backwards over the anterior zygapophyses of the adjoining posterior vertebra. The neural spine is rod-like with a distinct anterior keel, and with very little bilateral compression. This agrees very closely, both in cross-section and in proportions with that of the Recent genus. The transverse process is directed sharply upwards, and has an oval, concave facet for the articulation of the tubercle of the rib. This facet is turned

FIG. 2. (a) *Myorycteropus africanus*. Atlas vertebra. ×⅟₁. (b) *Orycteropus afer*. Atlas vertebra. ×½.

slightly backwards, instead of forwards as in *Orycteropus*, and the articular tubercle of the rib is correspondingly more pronounced, though less massive. The centra are rather shallower, but in general form these vertebrae approximate very closely to those of the existing genus.

Three of the anterior caudal vertebrae are preserved, and, although showing slight post-mortem distortion, are nearly complete. They appear to be Nos. 1–3, and the epiphyses, although held in position by the mineral matrix, are incompletely fused. In No. 1 the neural spine is intact and is relatively longer than that of the first caudal vertebra of the Recent animal. The zygapophyses are practically identical with those of *Orycteropus* except for their smaller size. The transverse processes are less flattened dorso-ventrally, but in no case is the whole of the process preserved, so that the degree of terminal splaying cannot be gauged. These three vertebrae are united by matrix in approximately their correct relative positions. The total length of the three centra together is 48 mm., as compared with 77 mm. for the first three caudal vertebrae of *Orycteropus*; a proportion of 62%.

Several rib fragments are preserved, but only four examples, all from the right side, have part of the head and the articular tubercle. The latter is not a massive rounded projection as that of *Orycteropus*, but forms a sharp posterior process, with

the articular facet on the dorsal part. These fragments appear to be Nos. 5–8. The shaft of No. 13 of the right side is nearly complete, and is very similar to that of the Recent animal, but both extremities are missing.

Shoulder girdle

A large part of each scapula is preserved (Text-fig. 3), and although the more fragile coracoid border is largely lost in both bones, the general shape and appearance is still reasonably clear, and is very similar to that of *Orycteropus*. The glenoid has exactly the same outline and curvature, and measures 20×12 mm., as compared with an average of 33×20 mm. in the Recent genus. The coracoid is rather less well developed than it is in the existing animal; whereas in the latter it is separated from the glenoid edge by a sharp groove, in the fossil it slopes back from the edge

FIG. 3. *Myorycteropus africanus*. Right scapula. $\times \frac{1}{1}$.

towards the blade. In *Orycteropus* the coracoid projects further downwards and forwards, away from the blade of the scapula, so that the forward edge unites with the coracoid border in a smooth curve. In the fossil it is more at right angles to the axis of the scapula, and thus more sharply distinct from the anterior blade. The acromion and metacromion are very well developed, but whereas in *Orycteropus* the edge opposite to the metacromion is practically straight, in the fossil it is expanded anteriorly. This suggests a strong trapezius in direct opposition to the powerful

deltoid. The measurements of the scapula compared with similar measurements of the right scapula of *O. afer lademanni*, are :

				Myorycteropus	*Orycteropus*	Proportion
Maximum length*	.	.	.	83 mm.	157 mm.	53%
,, breadth	.	.	.	50	93	54%
Length of glenoid	.	.	.	20	33	60%
Breadth ,, ,,	.	.	.	12	20	60%
Length of acromion	.	.	.	30	53	57%
Breadth† ,,	.	.	.	18	32	56%

* Maximum length, from tip of coracoid to posterior angle of glenoid edge.
† Maximum breadth, including metacromion.

The right clavicle is preserved complete (Text-fig. 4). The sternal end is relatively more enlarged than that of the same bone of *Orycteropus*, and the curvature of the shaft is somewhat more marked. In other respects the structure is almost identical with that of the Recent genus except for the smaller size. There seems to be some doubt about the articulation of this bone. According to Flower (*An Introduction to the Osteology of the Mammalia*, 1885) the expanded end articulates with the sternum,

FIG. 4. (*a*) *Myorycteropus africanus*. Right clavicle. × ⅟₁. (*b*) *Orycteropus afer*. Right clavicle. × ½.

and British Museum specimens agree with this. On the other hand a photograph of a mounted skeleton of *O. gaudryi* (Colbert, 1941, fig. 20) in the American Museum of Natural History shows the expanded end articulating with the acromion process of the scapula. The articular facets of the bone do not make this point clear, and for the present it is assumed that the expanded end of the clavicle is sternal. Comparative measurements of the right clavicle, in millimetres, are as follows:

				Myorycteropus	*Orycteropus*	Proportion
Maximum length	.	.	.	57·0	81·0	70%
Median a–p breadth	.	.	.	5·5	7·5	73%
,, transverse breadth	.	.	.	3·5	5·0	70%

It is significant that whereas the scapula and long-bones of *Myorycteropus* range from 46 to 53% of the corresponding bones of *O. afer*, the clavicle is 70% of its modern counterpart. In man the size and form of the clavicle is largely dependant upon the habits of the individual, and its strength is in direct proportion to the amount of manual work performed. Although man does not habitually dig with the hands, it is a reasonable assumption that the increased freedom of movement allowed by the

greater length of the clavicle would be advantageous to an animal of such fossorial habits. It is also consistent with the evidence, supplied by the scapula and humerus, of powerful shoulder muscles.

FRONT LIMB: HUMERUS.—The humerus of either side is well preserved (Text-fig. 5) and, apart from size, is somewhat similar to that of *Orycteropus* except for the excessive distal expansion, and the sharp curvature of the shaft. In the fossil the shaft is relatively more slender, and the head is thus more distinct. On the anterior border the deltoid ridge is very pronounced, and occupies a relatively larger area than that of the Recent animal. This indicates a very powerful deltoid muscle, which was also directly responsible for the curvature of the shaft. In the Recent genus the posterior
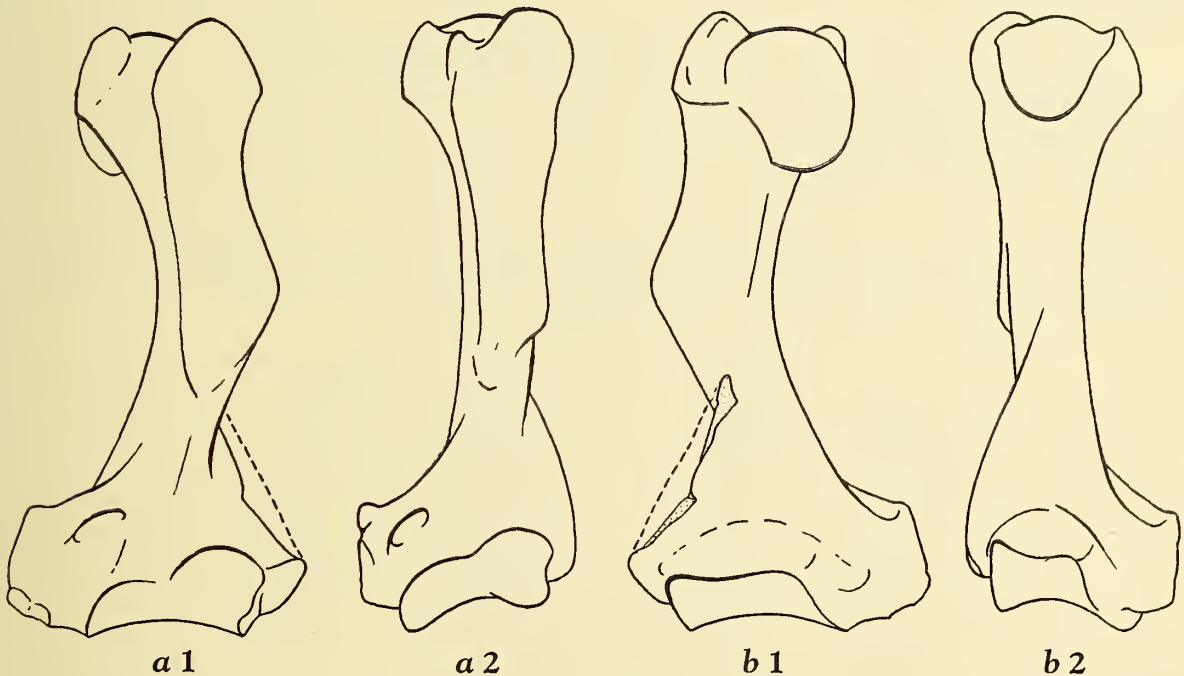
FIG. 5. (*a*) I. *Myorycteropus africanus*. Left humerus (anterior). ×¼. (*a*) 2. *Orycteropus afer*. Left humerus (anterior). ×½. (*b*) I. *Myorycteropus africanus*. Left humerus (posterior). ×¼. (*b*) 2. *Orycteropus afer*. Left humerus (posterior). ×½.

surface of the upper part of the shaft has a smooth curve, but in the fossil there is a ridge passing down from the head to merge with the very prominent supinator ridge. This is somewhat damaged in both specimens, but it was evidently very well developed, and reflects a strong triceps. A corresponding ridge on the postero-internal border arises from about the lower one-third of the shaft and curves inwards as a sharp flange behind the entepicondylar foramen. The tuberosities, and the condylar structure are practically identical with *Orycteropus*, but the entepicondylar region is somewhat more developed; consequently the relative breadth of the distal end of the bone is considerably greater. Indeed the breadth of the distal end is 48·8% of the total length of the bone, whereas in *Orycteropus* it is about 35%. In

Manis the degree of expansion is nearly as great (about 45%) owing to the greater development of the entepicondylar region.

Comparative measurements of the humerus, in millimetres, follow:

	Myorycteropus		*Orycteropus*	Proportion
	Right	Left		
Maximum length* . . .	83	81	162	51%
A–p length of head† . . .	25·5	24·5	42	60%
Transverse breadth of head‡ .	21	—	39	54%
Median a–p thickness of shaft§ .	15	15	25	60%
Median transverse breadth . .	9	9	18	50%
Maximum transverse breadth of distal end	—	39·5	57	69%

* From top of great tuberosity to lowest point of entepicondyle.
† Including great tuberosity.
‡ Including lesser tuberosity.
§ At base of deltoid ridge.

FORE-ARM.—The radius and ulna of the left side are preserved in good condition, though the olecranon process of the latter is missing. The two bones of the right fore-arm are also present, but badly damaged.
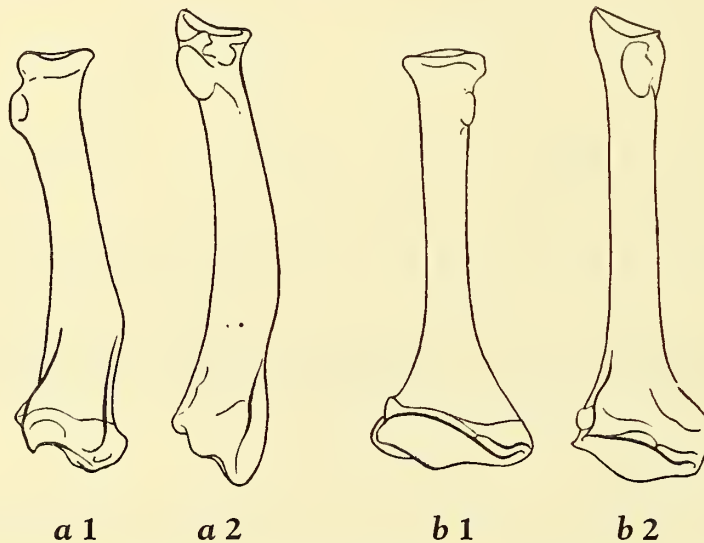

a 1   *a* 2   *b* 1   *b* 2

FIG. 6.   (*a*) 1. *Myorycteropus africanus*. Left radius (internal).   ×¼. (*a*) 2. *Orycteropus afer*. Left radius (internal).   ×½. (*b*) 1. *Myorycteropus africanus*. Left radius (posterior).   ×¼. (*b*) 2. *Orycteropus afer*. Left radius (posterior).   ×½.

In the radius (Text-fig. 6), the surface for articulation with the external condyle of the humerus is a simple oval set almost at right angles to the long axis of the shaft, whereas in *Orycteropus* the posterior corner of the articular surface is extended backwards, producing a pear-shaped facet which is distinctly oblique to the shaft. The

facets for articulation with the ulna are relatively smaller, and the shaft more slender than in *Orycteropus*. The distal end of the bone is more widely expanded in the fossil, and the anterior keel of the shaft more pronounced. Comparative measurements of the radius, in millimetres, are as follows:

	Myorycteropus	*Orycteropus*	Proportion
Maximum length . . .	55	120	46%
Minimum transverse thickness .	5·5	11	50%
Maximum a–p breadth (proximal)	9	16	56%
,, transverse ,, ,,	11	21	52%
,, a–p ,, (distal) .	15	26	58%
,, transverse ,, ,, .	22	35	63%
Ratio $\dfrac{\text{distal expansion}}{\text{maximum length}}$ . .	40%	29%	

The ulna (Text-fig. 7) has lost the olecranon process, so that the total length cannot be determined accurately. The surface for articulation with the humerus is more developed postero-internally, and the posterior part of the articular surface is slightly
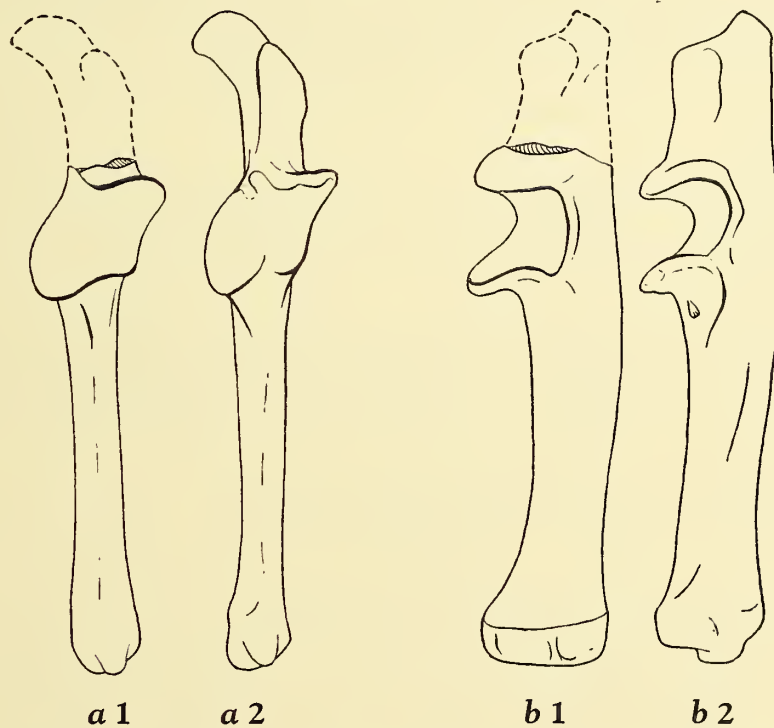

a 1   a 2   b 1   b 2

FIG. 7. (*a*) 1. *Myorycteropus africanus*. Left ulna (anterior). ×$\frac{1}{1}$. (*a*) 2. *Orycteropus afer*. Left ulna (anterior). ×$\frac{1}{2}$. (*b*) 1. *Myorycteropus africanus*. Left ulna (external). ×$\frac{1}{1}$. (*b*) 2. *Orycteropus afer*. Left ulna (external). ×$\frac{1}{2}$.

less developed. This would allow for the fore-arm to be more fully extended, and whereas in *Orycteropus* the maximum extension would give an angle of about 135° between arm and fore-arm, in the fossil this angle was at least 150°.

The facet for the articulation of the cuneiform extends further forwards, and almost unites with that for the radius. The shaft of the bone is relatively stouter and less compressed.

Comparative measurements of the ulna, in millimetres, are:

	Myorycteropus	Orycteropus	Proportion
Length*	63·5	125	51%
Minimum transverse thickness .	6	10	60%
,, a–p ,, .	11	21	52%
Maximum transverse thickness (distal)	10	16	62%
Maximum a–p thickness (distal) .	18	30	60%

* Measured from the posterior border of the humeral articulation to the most distal point of the shaft.

CARPUS.—The right trapezium is the only bone of the carpus to be preserved (Text-fig. 8). This is very similar to that of *Orycteropus* except that the antero-internal surface is relatively shorter, and is not produced down the inner surface of Mc. II to the same extent. There is no trace of a facet for even a vestigial Mc. I, and it is thus evident that the pollex was already suppressed.
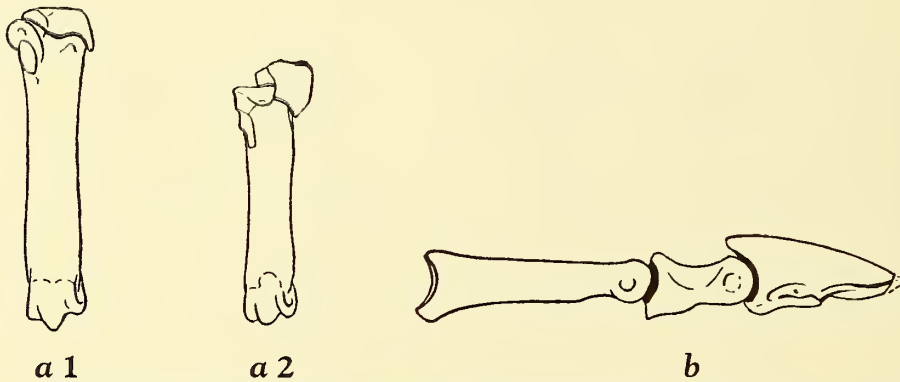

a 1   a 2   b

Fig. 8. (*a*) 1. *Myorycteropus africanus*. Right trapezium and Mc. II. ×¼. (*a*) 2. *Orycteropus afer*. Right trapezium and Mc. II. ×½. (*b*) *Myorycteropus africanus*. Left anterior digit II. ×1.

METACARPUS.—Only two bones of the metacarpus of the holotype are preserved, namely the second metacarpal of both sides (Text-fig. 8). The greater part of the proximal surface was occupied by the trapezium. The area for the articulation of the trapezoid is very much smaller than that of the modern animal, and is in the form of a narrow, rounded ridge, lying antero-posteriorly along the outer edge of the upper surface, adjacent to Mc. III. The facets at the top of the external surface of the shaft, for the articulation of Mc. III, are somewhat larger relatively than those of the Recent genus. In proportion to the limb bones the metacarpals are relatively longer, and have less antero-posterior compression than those of *Orycteropus*.

An isolated left Mc. V was obtained from the deposits of the Kathwanga series in 1947 (475 '47). This is very similar to that of *Orycteropus*, but the proximal end

lacks the lateral extension and the facet for articulation with the unciform is thus relatively smaller. The shaft is triangular in transverse section with sharp anterior and posterior external angles and a more rounded internal angle. The distal articulation is almost exactly similar to that of the modern animal, and is off-set from the shaft at the same angle.

Comparative measurements of the metacarpals, in millimetres, are:

	Myorycteropus	*Orycteropus*	Proportion
Mc. II			
Maximum length . . .	38	60	63%
Minimum transverse thickness .	6	10·5	57%
,, a–p ,, .	6	9	66%
Mc. V			
Maximum length . . .	16·75	26·25	64%
Minimum transverse thickness .	9·0	10·75	84%
,, a–p ,, .	7·5	10·50	71%

PHALANGES.—The proximal phalanges of both the second digits are preserved intact; they are very similar to those of *Orycteropus*, and, although relatively somewhat larger, the proportions are practically the same. Only the proximal half of the first phalanx of the third digit, and a rather crushed example of that of the fourth digit, both from the left side, are included. The structure is again very similar to that of *Orycteropus*.

Only one middle phalanx is preserved; it appears to be from the second digit of the left side. The dorsal surface of the bone has a distinct longitudinal ridge which is not present in the corresponding bone of *Orycteropus*, but in other respects there is little difference in structure.

The distal phalanges are identified as belonging to the second, third and fourth digits of the right side, and the second, fourth and fifth digits of the left side. The general structure is very similar to that of the corresponding bones of *Orycteropus*, but they are all slightly more compressed laterally, and the plantar protuberance is longer and narrower. In each example the extreme tip is broken, so that exact lengths are not available. The three bones of the second anterior digit are shown in Text-fig. 8b.

Comparative measurements of the phalanges, in millimetres, are as follows:

	Myorycteropus	*Orycteropus*	Proportion
Maximum length of Ph. II. 1 .	30	43	70%
Median a–p breadth ,, .	6·5	9·5	68%
,, transverse ,, ,, .	6·0	9·0	66%
Maximum length of Ph. IV. 1 .	22 (est.)	34	65%
Median a–p breadth ,, . .	8	11	73%
,, transverse ,, ,, . .	6·5	9	72%
Maximum length of Ph. II. 2 .	14	21	66%
,, ,, ,, Ph. II. 3 .	25 (est.)	34	73%
,, ,, ,, Ph. III. 3 .	27 (est.)	39	69%
,, ,, ,, Ph. IV. 3 .	20 (est.)	34	60%

PELVIC GIRDLE.—Parts of both innominates are preserved, including the acetabulum and part of the ischium of both sides, and most of the ilium of the right side. The general structure is very similar to that of *Orycteropus* but the bones are distinctly more slender. The pubis is broken immediately below the acetabulum, and the ischium is broken just in front of the ischial tuberosity, so that the shape of the obturator foramen is uncertain. Below the acetabulum, a large process, which is apparently derived from the anterior part of the pubis, is directed forwards and inwards. This is relatively less pronounced than the corresponding process of *Orycteropus*. The upward flange of the ilium is broken, but it appears to have been very similar. The area of the sacro-iliac articulation is slightly smaller relatively than in the Recent genus. Few detailed measurements can be obtained owing to the absence of all the extremities, but the general size appears to have been about half that of *Orycteropus*, e.g.:

	Myorycteropus	*Orycteropus*	Proportion
Length of acetabulum . . .	22 mm.	40 mm.	55%
Length of sacro-iliac articulation . .	31	61	51%
Minimum vertical thickness of ischium .	6·5	12·5	52%
Minimum transverse thickness of ischium	14·5	25·5	57%

a 1 a 2 b 1 b 2

FIG. 9. (*a*) 1. *Myorycteropus africanus*. Right femur (anterior). ×$\frac{1}{1}$. (*a*) 2. *Orycteropus afer*. Right femur (anterior). ×$\frac{1}{2}$. (*b*) 1. *Myorycteropus africanus*. Left tibia (anterior). ×$\frac{1}{1}$. (*b*) 2. *Orycteropus afer*. Left tibia (anterior). ×$\frac{1}{2}$.

HIND-LIMB.—FEMUR (Text-fig. 9). The right femur is complete except for the lower articulation, but this portion is preserved in that of the left side, of which only the lower one-third remains. In the diagram, a drawing of the left distal extremity has been reversed and superimposed on a drawing of the right shaft and head. Both specimens are somewhat crushed, but the structure is still visible. The shaft is more slender, and the head is thus more distinct and rounded. The great trochanter is rather less massive than that of *Orycteropus*; consequently if the bone be held with the shaft vertical, the top of the head is slightly above the level of the trochanter, whereas in the Recent animal the trochanter is the higher. In the fossil the trochanter is connected with the head by a very narrow neck, and there is a deep dividing notch which is practically absent in *Orycteropus*. On the other hand the posterior border is more developed, and is pulled inwards to overhang a deep digital fossa. The lesser trochanter is again less massive, but is appreciably more prominent. It is connected by a sharp ridge with a protuberance on the postero-internal border of the shaft slightly above the middle point. The third trochanter is relatively very much larger in the fossil. Thus the muscular development of the thigh of *Myorycteropus* was evidently very powerful. The outer condyle is somewhat distorted, but it was similar in form to that of *Orycteropus*, and the remainder of the distal end is almost identical except for the smaller size. Comparative measurements of the femur, in millimetres, are:

	Myorycteropus	*Orycteropus*	Proportion
Maximum length . . .	108 (est.)	202	53%
A–p length of head . . .	18	32	56%
Transverse length of head . .	21	39	54%
Median a–p breadth of shaft .	13·5	25	54%
Median transverse* ,, ,, .	22	38	58%
A–p breadth of distal end . .	33	62	53%
Transverse ,, ,, ,, ,, . .	35	61	57%

* Including the third trochanter.

The upper two-thirds of the left tibia and part of the shaft of the right are preserved, but neither example is complete and both are somewhat crushed. The proximal articular surfaces appear to have been similar in form to those of *Orycteropus*, but the outer facet is broken antero-posteriorly across the middle, and no point of contact for the fibula is preserved, though it is probable that the two bones were ankylosed in this region. The upper part of the shaft is even more flattened than in the Recent genus, and the median vertical ridge on the fibula side is less prominent. The length of the fragment is 73 mm. In four limbs of *Orycteropus* examined, the average tibia:femur proportion is 95%. Thus if the ratio were approximately the same in the fossil, the total length would have been about 103 mm. The left tibia and fibula have been reconstructed diagrammatically in Text-fig. 9. Comparative measurements of the upper part of the tibia, in millimetres, are:

	Myorycteropus	*Orycteropus*	Proportion
A–p breadth of proximal end . .	36	57	63%
Transverse breadth below fibula contact	11	33	33%
Median a–p breadth of shaft . .	11	25	44%
Median transverse ,, ,, ,, . .	9	18	50%

FIBULA.—Parts of both fibulae are preserved, but in each case the upper epiphysis was incompletely fused, and is missing, and neither example is complete. The bone of the left side is represented by two fragments, the upper section measuring 52 mm. in length. The proximal end is very much compressed bilaterally, and the front edge is somewhat damaged. Towards the middle of the shaft the cross-section becomes triangular. The distal section measures 31 mm. in length, and evidently only a few millimetres of the shaft is missing. The external malleolus is very prominent, but the posterior part of the distal articulation is less pronounced than in *Orycteropus*, suggesting that the area of articulation with the calcaneum was small. The facet for articulation with the astragalus is very similar in shape to that of the Recent genus. Comparative measurements of this bone, in millimetres, are:

	Myorycteropus	*Orycteropus*	Proportion
Probable total length . .	90	175	51%
Proximal a–p breadth* . .	19	37	51%
Proximal transverse ,, . .	5	7·5	66%
Median a–p ,, . .	6	8·5	70%
Median transverse ,, . .	6	7	86%
Distal a–p ,, . .	14·5	21	69%
Distal transverse ,,† .	16	23	70%

* Excluding the epiphysis.   † Including external malleolus.

TARSUS (Text-fig. 10).—The left tarsus is complete, with the exception of the internal cuneiform, and minor superficial damage to some of the individual bones. The astragalus is in good condition, and differs somewhat in proportions from that of *Orycteropus*. The inner flange of the surface for articulation with the tibia is relatively small, and the bulk of the articulation must have been on the external flange. The head is relatively more pronounced, but less spherical, being somewhat flattened dorso-ventrally. The internal surface is more vertical, and the facet for the articulation of the internal malleolus is flat and inconspicuous, whereas in *Orycteropus* it is larger, and distinctly concave. On the plantar surface, the external facet for articulation with the calcaneum is relatively larger, and the inner facet is nearly round, and slightly convex. Between these two facets lies a foramen which appears to perforate the posterior part of the body of the bone. Comparative measurements of the astragalus, in millimetres, are:

	Myorycteropus	*Orycteropus*	Proportion
Maximum length (diagonal) .	28	45	62%
Maximum breadth . .	21	36	58%
Transverse breadth of head .	12	16	75%
Maximum depth of head .	7·5	17	44%

The calcaneum has all the articular area preserved in good condition, but most of the tuber calcis is missing. The facets for the articulation of the astragalus are the normal counterparts of those already described, but on the dorsal surface the facet for the fibula curves sharply backwards and downwards into a distinct concavity on the upper surface of the tuber calcis. The facet for the cuboid is very similar in

shape to that of *Orycteropus*, but is less deeply concave. The facet for the navicular is largely obliterated, but since the opposing facet on the navicular is well developed it is clear that the articulation between these two bones was similar to that of the
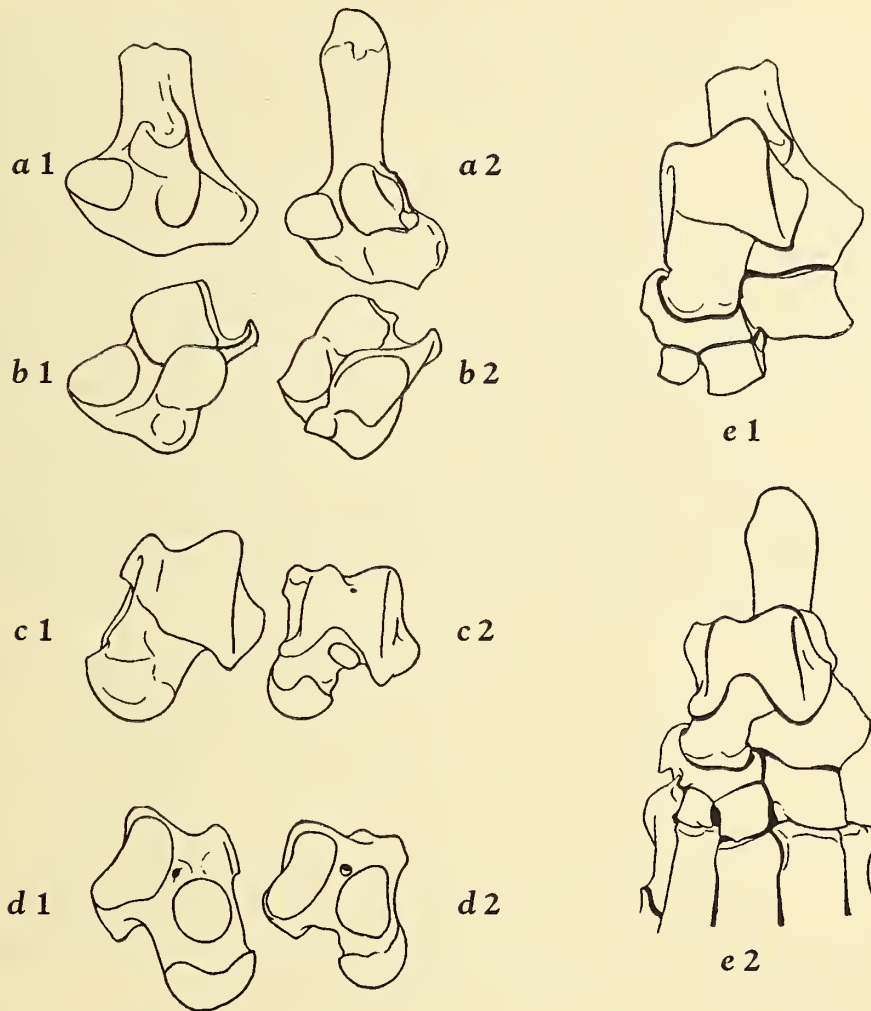

FIG. 10. (a) 1. *Myorycteropus africanus*. Left calcaneum (dorsal). ×$\frac{1}{1}$. (b) 1. *Myorycteropus africanus*. Left calcaneum (distal). ×$\frac{1}{1}$. (c) 1. *Myorycteropus africanus*. Left astragalus (dorsal). ×$\frac{1}{1}$. (d) 1. *Myorycteropus africanus*. Left astragalus (ventral). ×$\frac{1}{1}$. (e) 1. *Myorycteropus africanus*. Left tarsus (dorsal). ×$\frac{1}{1}$. (a) 2. *Orycteropus afer*. Left calcaneum (dorsal). ×$\frac{1}{2}$. (b) 2. *Orycteropus afer*. Left calcaneum (distal). ×$\frac{1}{2}$. (c) 2. *Orycteropus afer*. Left astragalus (dorsal). ×$\frac{1}{2}$. (d) 2. *Orycteropus afer*. Left astragalus (ventral). ×$\frac{1}{2}$. (e) 2. *Orycteropus afer*. Left tarsus (dorsal). ×$\frac{1}{2}$.

existing genus. On the external surface of the calcaneum the tubercle for the attachment of the calcaneo-fibular ligament is very prominent, and the tip is curved sharply upwards. The maximum breadth of the bone, from the outer point of this tubercle to the inner border of the sustentaculum is 26·5 mm., as compared with

42 mm. in the calcaneum of *Orycteropus*. The vertical depth of the tuber calcis at a point immediately behind the articular surface is 13·5 mm., and the transverse thickness 9 mm., compared with 25 mm. and 11·5 mm. respectively for the corresponding measurements in the Recent animal.

The navicular is very similar to that of *Orycteropus*, except that the main proximal facet is more oval, owing to the less spherical form of the head of the astragalus. The facets for the articulation with the calcaneum and the cuboid are widely separated from one another, whereas in *Orycteropus* they are inclined to be contiguous.

The cuboid is of the same general shape as that of the Recent genus, and the surfaces for articulation with the other bones of the tarsus are almost identical. On the lower surface the articular facet for Mt. IV is relatively larger, which suggests that the latter may have been more nearly equal to Mt. III than in *Orycteropus*.

The second and third cunieforms are practically identical in structure to those of the Recent genus, from which it is again evident that the general pattern and arrangement of the bones of the hind foot have undergone no major modification.

The first cuneiform and all the metatarsals are missing, and only three bones of the posterior digits are preserved. These appear to be the first and second phalanges of the left second digit, and the ungual phalanx of the right fourth digit. The latter was not associated with the skeleton. The plantar protuberance in this case is somewhat more rudimentary, but in other respects these bones show no significant dissimilarity from those of *Orycteropus* except as regards size. The comparative lengths of these bones, in millimetres, are:

Maximum length of—				*Myorycteropus*	*Orycteropus*	Proportion
Cuboid	.	.	.	13	21·5	60%
Navicular	.	.	.	13·5	26	52%
Cuneiform 3	.	.	.	17	26	65%
Cuneiform 2	.	.	.	10	20	50%
Ph. II. 1	.	.	.	27	42	64%
Ph. II. 2	.	.	.	14	21	66%

PROPORTIONS.—The following is an analysis of the comparative lengths of the principal limb bones of *Myorycteropus* and *Orycteropus*.

Maximum length of—				*Myorycteropus*	*Orycteropus*	Proportion
Scapula	.	.	.	83	157	53%
Humerus	.	.	.	83	162	51%
Radius	.	.	.	55	120	46%
Ulna	.	.	.	63·5	125	51%
Femur	.	.	.	108	202	53%
Ratio—Ulna:Humerus	.	.		76%	77%	
Humerus:Femur	.			77%	80%	

This shows that the general size of the animal was little more than half that of an average example of *Orycteropus afer lademanni* Grote; the species at present living in the area.

On the other hand a similar analysis of the few available bones of the metacarpus and phalanges reveals that these were about two-thirds of the size of the corresponding bones of the Recent species.

Maximum length of—	*Myorycteropus*	*Orycteropus*	Proportion
Mc. II.	38	60	63%
Ph. II. 1 (anterior) . .	30	43	70%
Ph. II. 2 ,, . . .	14	21	66%
Ph. II. 1 (posterior) . .	27	42	64%
Ph. II. 2 ,, . . .	14	21	66%

The ungual phalanges are quite as fully developed as those of the Recent animal, and since the proportionate size of the feet was greater, it is clear that the digging-power of the species was already very highly developed.

COMPARISON WITH OTHER FOSSIL MATERIAL.—I am indebted to Professor Millot and Dr. Paulian for the loan of certain specimens of *Plesiorycteropus* from Madagascar, by which a direct comparison can be made of the structural difference in the limb bones of the two genera.

In *Plesiorycteropus* the shaft of the humerus is more slender and less sharply bowed; the deltoid ridge is less pronounced and extends for less than half the length of the shaft, whereas in *Myorycteropus* it occupies nearly two-thirds of the total length. The expansion of the distal end is also less, so that the maximum breadth is the equivalent of about 35% of the total length, as in *Orycteropus*, whereas in the Miocene genus it is as much as 48·8%.

The most striking difference between the radii is the extreme lateral compression of the shaft, resulting in sharp anterior and posterior ridges in the Madagascar genus, and the smaller degree of expansion of the distal end, which is only 25% of the total length, as compared with 40% in *Myorycteropus*.

In the ulna the position is almost reversed, since there is very little lateral compression of the shaft in *Plesiorycteropus*, and whereas in both the Recent and the Miocene genera the shaft is of even depth and the distal end considerably expanded antero-posteriorly, in the Malagasy genus the shaft tapers almost to a point at the distal end.

The head of the femur is much smaller in *Plesiorycteropus*, and more detached from the shaft by reason of the long, slender neck. The great trochanter is very much more slender and elongated than in *Myorycteropus* and the lesser trochanter is considerably larger, whilst the third trochanter is small. The latter is continuous with a sharp outer ridge which merges with the great trochanter, and which is entirely absent in both the Recent and the Miocene genera.

The tibia and fibula are not well preserved in *Myorycteropus*, yet it is clear from the fragments of the fibula that the two bones were contiguous, but not fused at the distal ends, and that the condition must have been very similar to that in *Orycteropus*. In *Plesiorycteropus*, however, there is complete fusion for 20% of the total length, and the whole of the distal region of both bones is considerably flattened antero-posteriorly, which is not the case in the Recent genus, nor in the fibula of *Myorycteropus*.

The only other comparable bone is the astragalus, which in *Plesiorycteropus* is flatter dorso-ventrally.   The head is also much shorter and less clearly differentiated, and there is no trace of the foramen which penetrates the body of the bone in *Orycteropus*.

It is clear from the above that there is no very close connection between *Plesiorycteropus* and *Myorycteropus*, and indeed the latter appears to be much more closely similar to the Recent genus than to the sub-fossil form from Madagascar.

There appears to be a certain similarity between the humerus of *Myorycteropus* and that of *Palaeorycteropus* Filhol, from the Quercy deposits.   Referring to the proximal end of the humerus in the latter, Filhol (1894) states that "les tubérosités externe et interne, entre lequelles passe la gouttière bicipitale, sont très détachées, ces mêmes saillies s'effacent sur notre fossile".   In *Myorycteropus* these tuberosities are quite as fully developed as those of the Recent genus.   Moreover, to judge by Filhol's figure, the shaft of the humerus is straighter in *Palaeorycteropus*, and the distal expansion is only equal to about 33% of the total length.

The species *Orycteropus depéreti* Helbing (1933) from the Lower Pliocene of Perpignan, although somewhat smaller than the Recent species, is still considerably larger than *Myorycteropus*.   The length of the upper molar series is given as 33 mm., whereas in the Miocene genus it is only 23·5 mm.   Since only part of the maxilla of *Myorycteropus* is preserved, further direct comparison with the Lower Pliocene species is impossible, but evidently the latter was structurally similar to Recent species of *Orycteropus*, and the ascending ramus of the mandible must also have been higher and more upright than that of *Myorycteropus*.

Conclusions.—Extensive study of the internal structure of the teeth shows that there is no essential difference in development and formation between the teeth of *Myorycteropus* and those of *Orycteropus*.   Since the peculiar columnar structure of the dentine was already in evidence in the Lower Miocene, it is probable that the evolutionary process has been extremely slow, and that the earliest stages of its development are likely to have been in the Eocene period or earlier.   Several theories have been put forward to account for this unique structure, but as yet no explanation offers a satisfactory solution of all the problems involved.   It is hoped that work now in progress will settle at least some of the outstanding questions.

The great muscular strength of the limbs of *Myorycteropus* has exaggerated most of the features which characterise the long-bones of *Orycteropus*, and one must therefore infer that the animal was even more highly adapted for digging than is the existing genus, and, consequently, that its mode of life must have been similar. In many other anatomical respects *Myorycteropus* appears to show a higher degree of specialization than does the Recent genus, particularly in the attenuation of the mandible and in the expansion of the distal ends of most of the limb bones.   According to Colbert (1941) the latter feature is one of the characters by which *Orycteropus* may be regarded as having progressed, if it has evolved from a primitive Condylarth condition.   The fact that the Lower Miocene genus exhibits an even greater degree of specialization in this respect suggests that if Colbert's view is correct *Myorycteropus* cannot be in the direct ancestral line to the Recent genus, but must represent an aberrant offshoot of a more primitive common ancestor.

Jepson (1932) has discussed at some length the historical background to the

problem arising from the taxonomic relationships of the Tubulidentata, and as he points out, by selecting one or two of the many highly specialized characters of the order, it has been possible to build up hypotheses by which *Orycteropus* may be derived from almost any of the early branches of the mammalia. On the other hand, whilst it may be true to say that the origin of the genus "remains a complete puzzle", there is a considerable weight of evidence to support the view that the Tubulidentata at least shared a common ancestry with the Condylarthra, and, as Colbert has shown, the evidence in favour of *Tubulodon* as being directly ancestral is by no means conclusive. It is easy, and often diverting, to speculate upon the evolution of such a group, but on the strength of one Eocene, one Miocene and a few Plio-Pleistocene specimens it is clearly impossible to do more than guess at the development which has taken place between the end of the Cretaceous period and the present day.

Orycteropus sp. indet.

In 1931, Hopwood (1954) found a single Aard Vark tooth when collecting from the Miocene deposits at Koru (Lat. 0° 10′ S.: Long. 35° 15′ E.), Kenya Colony. The tooth appears to be a left upper M^1, and is certainly not another example of *Myorycteropus*. It is slightly smaller than the corresponding tooth of a medium-sized specimen of *Orycteropus afer*, but in details of structure and wear it approximates very closely to that species. The anterior lobe, and half of the posterior lobe, is worn to a smooth, gently concave surface by contact with the lower M_1. Across the posterior lobe a sharp ridge separates the attrition surface produced by the lower M_2. Both lobes are slightly curved antero-posteriorly from crown to root, with a posterior convexity. In the Recent tooth there is also a gentle lateral curvature with a median convexity, whereas in the fossil this is not apparent. At the root, the open ends of the dentinal columns show the normal honey-comb structure, but these are not clearly visible at the crown as in *Myorycteropus*. The maximum height of the posterior lobe from crown to root is 15·75 mm., compared with 16·5 mm. in the Recent animal. The other dimensions of the tooth compared, in millimetres, with those of *O. afer* and with *Myorycteropus* are as follows:

| M^1 | | Maximum length | Maximum breadth at— | | | Index |
			Anterior lobe	Con-striction	Posterior lobe	
Koru specimen	.	10·75	6·50	4·25	6·50	60
O. afer .	.	11·40	7·25	4·75	7·25	63
Myorycteropus	.	7·20	4·70	2·70	4·50	65

It has been pointed out above that *Myorycteropus* is probably not in the direct ancestral line of the Recent species, and if this view is correct it is reasonable to suppose that there must have been a contemporary Miocene representative of the group from which the Recent African species is derived. The tooth under discussion is so closely similar to that of *O. afer* that there can be no justification for separating it from the Recent genus. It is perhaps unlikely that the species *O. afer* has survived

unchanged from the lower Miocene, and it is thus possible that the Koru specimen should be assigned to a new species. On the other hand it would be impossible to give a satisfactory specific diagnosis, based on a single tooth which is nearly indistinguishable from that of an existing species. For this reason the Koru tooth is provisionally placed under the general heading *Orycteropus* sp. indet.

A NEW PLEISTOCENE SPECIES OF *ORYCTEROPUS*

In addition to the well-known Miocene fossiliferous deposits of Rusinga Island, pockets of Pleistocene gravel and alluvium occur in some places. In one of these, lying between Kiahera and Sienga hills, part of the skeleton of a species of *Orycteropus* was discovered in 1950. The bones were heavily encrusted with a rough concretionary material which in many cases obscured all trace of bone until the lumps were fractured. Consequently a great deal of the skeleton was not recovered, but a large part of the skull and mandible is sufficient to show that it represents a new species.

The relative scarcity of Pleistocene deposits on Rusinga Island, and the absence of stratigraphical data, prevents any exact determination of the horizon. Moreover there is at present no associated fauna from the isolated deposits from which this fossil was obtained. On the other hand, the evidence of fossils and stone-age implements in other parts of the island indicates that the majority of the post-Miocene deposits in the area belong to the end of the Middle-Pleistocene or later, and there is no reason to suppose that the fossil under consideration represents any earlier period.

Orycteropus crassidens sp. nov.

(Pl. **3**; Pl. **4**, figs. 4, 7; Text-figs. 11–13)

DIAGNOSIS.—An *Orycteropus* closely resembling *O. afer* Pall. but having relatively larger teeth.

HOLOTYPE.—Parts of a skull, mandible and associated skeleton (No. 1811 '50) from Rusinga Island.

HORIZON.—Pleistocene.

LOCALITY.—Rusinga Island (Kiahera-Sienga area), Victoria Nyanza, Kenya Colony. Lat. 0° 26′ S.: Long. 34° 9′ E.

MATERIAL.—The left side of the skull and both halves of the mandible; parts of the first six cervical vertebrae, one thoracic and two caudal vertebrae; fragments of the distal ends of both humeri and the proximal end of the right radius; three carpals, parts of three metacarpals and several anterior phalanges; a left astragalus, right first metatarsal and parts of three posterior phalanges.

REFERRED SPECIMEN.—Fragments of another skeleton of *Orycteropus* were collected in 1955 from the Pleistocene of Kanjera (Lat. 0° 20′ S.: Long. 34° 36′ E.), Kenya Colony. These represent a slightly larger animal than the holotype, but the molars are again relatively large, and the remains are therefore referred to *O. crassidens*.

The skull is shattered into more than 100 fragments, but part of the right maxilla is preserved, bearing the three molars. An upper Pm^4 is also included, and the left upper M^2. Two mandibular fragments show the roots of the lower fourth premolars; the right M_1 is complete, while a third fragment has part of the socket and root of M_3. The post-cranial skeleton is represented by the greater part of the vertebral column and numerous rib fragments; a well preserved humerus and most of the carpals, metacarpals and anterior phalanges. The hind limbs are not present, with the exception of the left patella and four posterior phalanges.

SKULL.—The holotype includes the greater part of the left side of the cranium and basi-cranium; the left orbit, maxilla and part of the palate (Pl. 3, figs. 1 & 3). The five left upper cheek teeth are preserved in good condition, and there is no trace of any additional anterior teeth in the 30 mm. of maxilla which remains in front of the tooth series. The animal was fully mature, and in size it appears to have been almost exactly similar to normal adult examples of *O. afer lademanni* Grote. Unfortunately the middle line is not preserved except at the base, so that the height of the skull, and the development of the frontal lobes cannot be determined. The anterior part of the maxilla is missing from a point 30 mm. in front of the tooth-row, and the alveolar edge in this region forms an even more pronounced ridge than in *O. afer*. The tooth-row contains two premolars and three molars, and measures 56 mm., as compared with an average length of 51·4 mm. in the Recent species. The infra-orbital foramen is situated above M^1. The anterior border of the orbit lies over M^3, as in the Recent species, but the orbit itself is more flattened on its antero-dorsal edge. The post-orbital process is missing, but it appears to have been prominent. The anterior part of the zygomatic arch is somewhat distorted, but it seems that there was practically no downward projection of the lower border at the point of contact between the maxilla and the jugal. The mastoid region is rather more developed in the fossil than in Recent examples. The transverse part of the maxillary-palatine suture lies at the level of the middle of M^1, whereas in the modern animal it is generally behind M^1.

It is unfortunate that many of the characters specifically discussed by Colbert (1941) in his study of *O. gaudryi* are not sufficiently well preserved in the new fossil for direct comparison to be made. It is apparent, however, that the general size of the animal was already equivalent to that of *O. afer*, and also that the attenuation of the muzzle had reached approximately similar proportions. Text-fig. 11 is a diagrammatic restoration of the outline of the skull.

UPPER DENTITION.—The five teeth are almost identical, both in form and in wear, with those of the Recent species, and differ only in their slightly greater size. Pm^3 is almost quadrate, with rounded angles; the widest point being at the back. Pm^4 and M^1 are so similar to the corresponding modern teeth that no description is necessary. In M^2 the lobes are less rounded, and they appear to be almost pointed at their outer and inner borders. The median transverse groove is also deeper; the constriction having exactly the same measurement as appreciably smaller teeth of *O. afer*. M^3 is relatively more elongated than that of the modern animal. In *O. afer* the upward projection of the root socket for M^3 is distinctly oblique to the plane of the palate when viewed from behind. In the fossil, the socket is practically perpen-
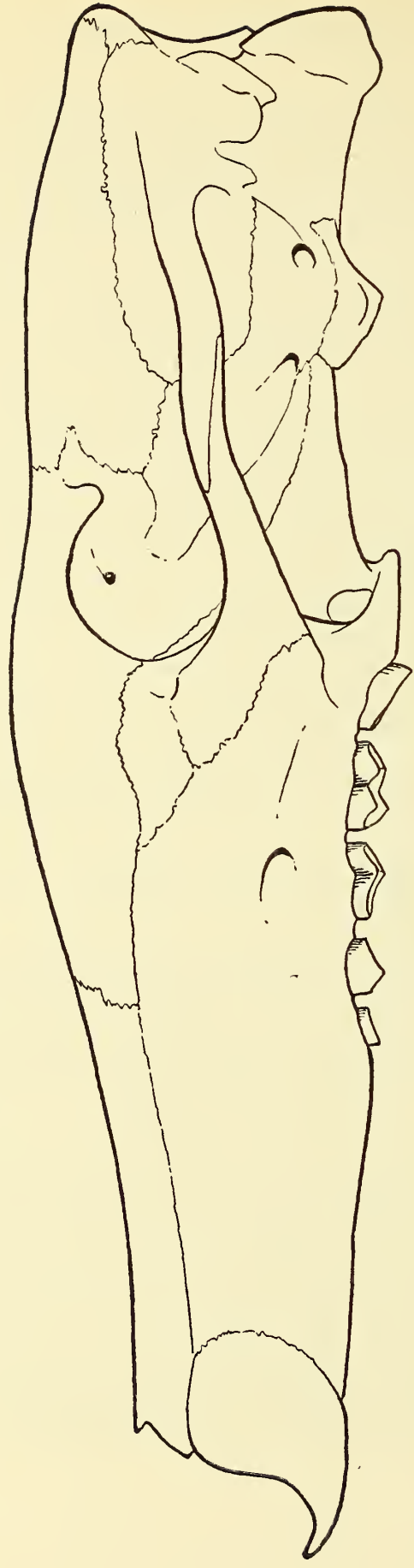
Fig. 11. Restoration of skull of *Orycteropus crassidens*. × ¼.

dicular to the plane of the palate (Text-fig. 12). This is consistent with Colbert's theory of a gradual expansion of the cranial region, by which the root sockets of the third molars would tend to become splayed outwards in the more highly developed Recent species.
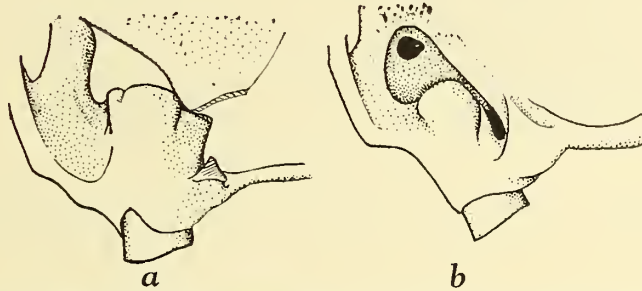

FIG. 12. (a) *Orycteropus crassidens*. Posterior view of left maxilla and socket for M³. ×$\frac{1}{1}$. (b) *Orycteropus afer*. Posterior view of left maxilla and socket for M³. ×$\frac{1}{1}$.

The measurements of the upper teeth, in millimetres, are:

	Maximum length	Maximum breadth Anterior lobe Posterior lobe		Index
Pm³ .	6·25 (5·6)	4·0 (3·0)		64 (54)
Pm⁴ . .	8·75 (7·4)	7·25 (5·6)		82 (76)
M¹ . .	12·0 (11·4)	8·5 (7·3)	9·25 (8·0)	77 (70)
M² . .	14·0 (12·4)	10·5 (8·5)	10·75 (9·0)	77 (73)
M³ . .	11·5 (9·9)	9·0 (7·5)		78 (76)
M¹—M³ .	38·5 (36·25)			
Pm³—M³ .	56·0 (51·4)			

The figures in brackets represent the average of the corresponding measurements in eight tooth-rows of *O. afer*.

MANDIBLE.—The left half of the mandible (Pl. 3, figs. 2 & 4) is complete except for the extreme anterior point and the tip of the coronoid process, and the whole of the horizontal ramus of the right side is also preserved. All the molars are complete; the fourth premolar of both sides is broken at the alveolar border, and there is no trace of a third premolar or of any additional anterior teeth on either side. It is estimated that the missing portion of the anterior symphysial area was about 5 mm. (Text-fig. 13).

The angle between the anterior border of the ascending ramus and the gingival edge is about 70° as in *O. afer*, but the antero-posterior depth of the ascending ramus is slightly less in the fossil. The condyle is more slender and elongated than that of the Recent animal, and is somewhat splayed backwards, so that the mandibular notch is wider. The coronoid process is more slender, and appears to have ended almost in a point, rather than with the somewhat square termination found in Recent mandibles. The horizontal ramus is very similar to that of *O. afer*, but is slightly less deep.

The mandibular measurements, in millimetres, are:

				O. crassidens	O. afer
Maximum length (from condyle)	.		.	212 (est.)	206
,, ,, (from angle)			.	208 (est.)	204
Depth of ramus behind M_3	.		.	22	23·5
,, ,, ,, at M_2	.		.	23	23·5
Minimum depth of ramus	.		.	14	14·5
Length of molar series	.		.	43	38·5
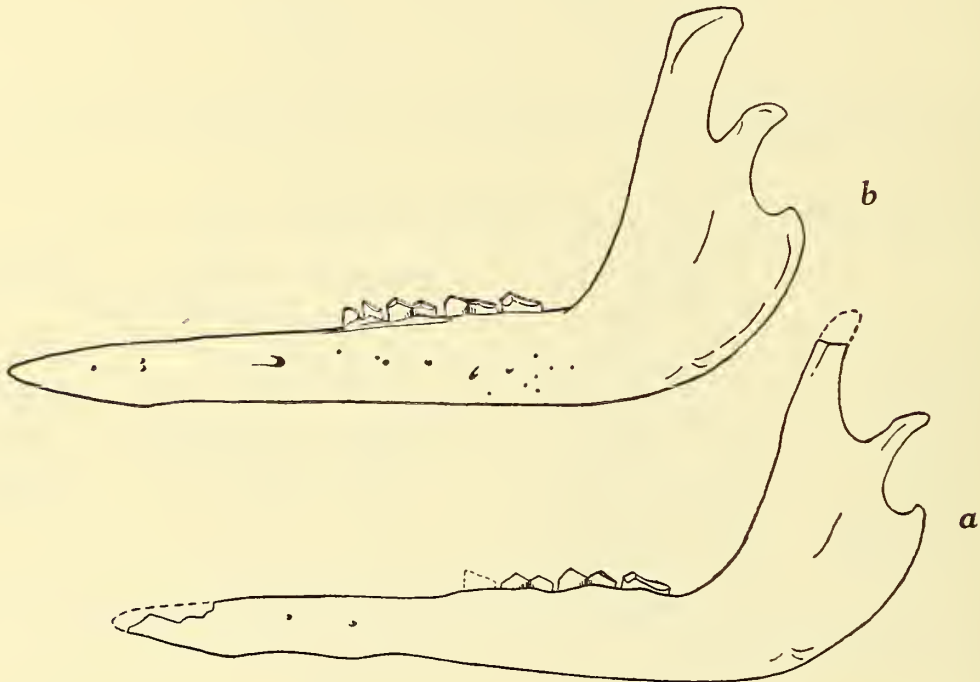
FIG. 13. (a) *Orycteropus crassidens*. Left mandibular ramus. ×½. (b) *Orycteropus afer*. Left mandibular ramus. ×½.

LOWER DENTITION.—The third premolar, if it was ever developed, must have been lost some considerable time before death, since no trace of the socket remains in either side of the mandible. In *O. afer* the presence or absence of this tooth is a variable character, but it is generally present.

The crown of Pm_4 of both sides is missing, but the cross section of the root at the alveolus shows that it was oval in shape, and much less compressed laterally than the Recent tooth. The three molars are almost exactly similar to those of *O. afer* except for their slightly larger size.

In all the lower teeth of *O. afer* examined, there is a distinct curvature of the vertical axis so that the anterior and labial borders are more or less concave from crown to root. In the fossil, all the lower teeth appear to be straight throughout

their vertical length, with no curvature in any direction. The measurements of the lower teeth, in millimetres, are as follows:

	Maximum length	Maximum breadth Anterior lobe	Posterior lobe	Index
Pm$_4$.	8·0 (6·8)	5·5 (3·7)		69 (54)
M$_1$.	13·75 (11·8)	8·0 (6·7)	9·5 (7·8)	69 (66)
M$_2$.	15·0 (12·9)	10·5 (8·8)	11·25 (9·2)	75 (71)
M$_3$.	12·25 (10·6)	9·75 (8·3)		79 (78)
Pm$_4$—M$_3$.	53·0 (46·75)			

The figures in brackets represent the average of the corresponding measurements in eight tooth-rows of *O. afer*.

The right second lower molar has been sectioned to show the columnar structure (Pl. 4, figs. 4 & 7); the internal arrangement of the dentinal columns is not appreciably different from that found in the Recent species, except that some of the peripheral columns are inclined to be isolated from the main body, although they are bound to the whole by the surface layer of cementum (Pl. 4, fig. 7). This supports the view that the inter-columnar matrix is normal cementum.

VERTEBRAL COLUMN.—The atlas vertebra is represented by a small part of the dorsal arch. This is somewhat more massive than the corresponding portion of a Recent example; the median antero-posterior breadth measuring 17 mm. as compared with 15·5 mm. The body of the axis vertebra is complete, and also the greater part of the arch, but with the exception of the right posterior zygapophysis all the lateral processes have been lost. The only post-cranial comparative material available of a Recent species is of a sub-adult animal in which everything is appreciably more slender, but the details of structure appear to be almost identical. The maximum length of the fossil bone, including the odontoid process, is 35 mm. compared with 32 mm. in the Recent animal.

The third cervical vertebra retains both the lateral processes and part of the neural arch, including the anterior and posterior zygapophyses of the right side. The centrum measures 16·5 mm. antero-posteriorly, compared with 15·25 mm. in the Recent bone, while the lateral processes show a marked elongation; the total transverse measurement across the process being 60 mm. in the fossil, and only 54 mm. in the Recent sub-adult example. The fourth, fifth and sixth cervicals are represented by the centra only, which again are more massive than those of the Recent species. The antero-posterior measurement of each is 16 mm., against 14·5 mm.

The thoracic vertebra consists of the centrum with the greater part of both transverse processes, but it lacks the whole of the neural arch. Antero-externally the facets for the articulation of the capitulum and tubercle of the rib are continuous. In the Recent *O. afer* this only occurs in the last three thoracic vertebrae. There is also a well-defined postero-external facet for part of the capitulum of the subsequent rib. The bone cannot therefore be the last or 13th thoracic vertebra, and the general size, both of the centrum and of the transverse process suggests that it is the 12th rather than the 11th. The transverse processes are relatively more massive

than those of the Recent animal, but in other respects there is very close resemblance between them.

The two caudal vertebrae appear to be the 8th and 9th. The neural arches are complete, but although their posterior processes are missing, they were evidently very small. All the processes of both vertebrae are missing with the exception of the left metapophysis of the 9th. This is distinctly larger than that of the corresponding bone in the Recent animal, but there is no trace of any facet for the articulation of the posterior process of the preceding vertebra. In *O. afer* this facet is usually visible up to, and including the 8th caudal, but thereafter contact is lost between the processes, although the neural arch remains complete in the first eleven caudal vertebrae. The centra of the two fossil bones are almost identical to those of *O. afer*.

FRONT LIMB.—The distal articular end of the left humerus is preserved, with part of the entepicondylar region from the right side, and also the proximal end of the right radius. These show no features by which they may be distinguished from the corresponding bones of *O. afer*, and detailed description is thus unnecessary. The same may be said of the bones of the manus. These include the right scaphoid and lunar; the left unciform; the proximal ends of the left metacarpals III and IV, and parts of eight phalanges. The right ungual of the third digit is preserved, and has the plantar protuberance very well developed. Thus the adaptation for digging, at least in the front limbs, was evidently in no way inferior to that of the Recent species.

HIND LIMB.—The only bones recovered are the left astragalus, the right first metatarsal and two phalanges. The astragalus is complete, and closely resembles that of *O. afer*. On the dorsal surface the inner flange of the tibia facet appears to merge gradually with the neck, whereas in the Recent species the anterior part of the facet ends abruptly in a sharp edge. On the upper surface of the neck the depression between the facets for the tibia and the navicular is much more pronounced in the fossil. The astragalar foramen penetrates the body of the bone in the usual manner.

The right Mt. I is almost exactly similar in structure to that of *O. afer*, but is slightly more massive in all dimensions. The comparative measurements of these two bones, in millimetres, are:

Astragalus	*O. crassidens*	*O. afer*
Maximum length (diagonal) . .	47·0	45·0
Maximum breadth at right angles .	37·0	36·0

Metatarsal I		
Maximum length	38·5	38·0
Proximal a–p breadth . . .	17·0	16·5
,, transverse ,, . . .	11·5	11·0
Median a–p breadth . . .	10·0	9·5
,, transverse ,, . . .	9·0	8·5
Distal a–p breadth . . .	12·5	12·0
,, transverse ,, . . .	13·0	12·0

No other bones of the holotype skeleton were recovered, but an ungual toe bone (No. 1218 '50) from the surface of the R.1a series of deposits is provisionally referred to this species.   By comparison with bones of *O. afer* it appears to be that of the left hind fourth digit, but it is quite distinct from any other terminal phalanges of the Recent species.   The upper surface consists of a rounded ridge as in the hind toes of the existing animal, but whereas in the latter the dorsal surface is longitudinally convex, in the fossil it is slightly concave, and the whole bone is thus flatter.   The dorsal ridge is also more clearly defined in the fossil, with the lateral flanges well differentiated, whereas in *O. afer* the flanges merge imperceptibly with the body of the bone on the upper surface, and, being directed rather more downwards, the whole bone is distinctly arched.   Consequently the plantar surface in the Recent species is concave and the plantar protuberance is very highly developed, but in the fossil the protuberance is almost non-existent and the whole of the lower surface is gently convex.   The proximal surface for articulation with Ph. 2 is more sharply oblique to the general plane of the plantar surface in the fossil, and it is divided by a distinct median vertical ridge, indicating that the distal articulation surface of Ph. 2 was somewhat bi-lobed and not cylindrical as in *O. afer*.   The dimensions of the bone are slightly less than those of the corresponding bone of *O. afer*.

Although the shape is typically that of *Orycteropus*, it may be regarded as a more generalized toe, lacking the high degree of specialization of the Recent animal. It is possible that in the latter the hind foot may play a more active part in digging, and has thus developed stronger and more arched terminal phalanges with more pronounced plantar protuberances.   On the other hand, since this bone was not found in association with the holotype skeleton it may represent a younger animal, or even an abnormality, and may not be characteristic of the normal adult condition of *O. crassidens*.

DESCRIPTION OF REFERRED SPECIMEN.—In the fourth pre-molar the crown appears to be undamaged, and is worn to a flat surface.   In Pm^4 of the Recent species, and in the holotype, the crown has two sub-equal attrition surfaces, produced by contact with the lower Pm_4 and with the anterior lobe of M_1.   A corresponding oblique surface of wear is thus normally found on both teeth, but in the fossil under consideration the occlusal surfaces of both show level wear.   The three upper molars have the usual transverse section, but the occlusal surfaces are again almost smooth. It is probable that the attrition pattern varies with the age of the animal.   The upper third molar is considerably elongated, as in the holotype.   In the mandible fragments there is no trace of any tooth-socket in front of Pm_4.

The bones of the post-cranial skeleton show no unusual features, and agree very closely with those of the holotype, though evidently of a slightly larger individual. The humerus is similar in size to that of the Recent West African form *O. erikssoni faradjius* Hatt, and the fact that the molars are larger even than those of the typical race *O. e. erikssoni* Lönnberg, adds support to the view that the tooth-size is specifically significant.

The ungual phalanges of the second and fourth hind digits are structurally identical with those of *O. afer*.   They bear little resemblance to the specimen No. 1218.'50 described above; evidently the latter is atypical, or it may, perhaps, represent a distinct species.

In view of the large size of this animal, the few available measurements, in millimetres, are compared below with those of *O. e. erikssoni* Lönnberg (1906), and of *O. e. faradjius* Hatt (Colbert, 1941).

Upper teeth	*O. crassidens*			*O. e. erikssoni*			*O. e. faradjius*		
	Lgth	Bdth	Ind	Lgth	Bdth	Ind	Lgth	Bdth	Ind
Pm^4	8·5	6·5	76	9·0	5·0	55	7·5	6·0	80
M^1	14·0	9·5	68	11·0	7·0	64	11·5	7·5	65
M^2	14·0	10·5	75	12·0	9·0	75	12·5	9·0	72
M^3	11·5	9·0	78	10·0	8·0	80	10·0	8·5	85
M^1–M^3	40·0			—			36·0		

Lower teeth									
Pm_4	7·5	5·0	66	8·0	5·0	62	6·0	4·0	66
M_1	15·0	9·0	70	11·0	7·0	64	11·5	8·0	70

Ramus depth at level of									
Pm_3*	18·0			—			17·0		
Pm_4	20·0			—			—		
M_1	23·5			—			22·0		
Humerus	175·0			182·0			174·0		
,, (distal)		64·5			70·0			62·0	

* Colbert took the depth at Pm_3; in the absence of this tooth in *O. crassidens* the depth given here was taken immediately in front of Pm_4.

Comparable measurements of the anterior digits of *O. erikssoni* are not available. Those of the third digit of *O. e. faradjius* (Colbert, 1941) are shown in brackets.

Anterior digits	II	III	IV	V
Metacarpal	68	69 (65)	51	29
Ph. 1	45	41 (39)	35	24
Ph. 2	21	21 (20)	22	17
Ph. 3	35	36 (35)	32	30*

* Measurement estimated.

CONCLUSION.—Examination of the Pleistocene skeleton shows that the animal was so closely similar to the Recent species that it would be impossible to find adequate grounds for considering it to be generically distinct. It may, however, be distinguished from Recent species of *Orycteropus* by a variety of characters, all of which may be regarded as less highly specialized. Moreover the teeth of this animal appear to be larger than those of any species hitherto described, either Recent or fossil. The African Pleistocene material described in this paper is therefore assigned to a new species, for which the name *Orycteropus crassidens* is proposed.

The accompanying table compares the dental measurements of the holotype of *O. crassidens* with those of *O. afer*, and also with those of the four fossil species of

Orycteropus previously known. These include *O. gaudryi* Major, from the Pontian deposits of Samos; already compared with the new African species. In addition, the species *O. browni* Colbert and *O. pilgrimi* Colbert have been described from the Middle Siwalik deposits of the Punjab. *O. browni* is a small species, with a greatly reduced M^3 which appears to have little similarity to that of the new species. *O. pilgrimi* is distinguished by straight anterior and posterior surfaces of the lower M_2, and a relatively shallow vertical indentation of the lingual surface. Neither of these characters is present in *O. crassidens*, which is therefore regarded as specifically distinct. The fourth species, *O. depéreti* Helbing, was found in Pliocene deposits in France. This is again a comparatively small species and is readily separable from the new African species by the presence of five upper pre-molars.

UPPER TEETH	Pm3		Pm4		M1		M2		M3	
	Lgth	Bdth	Lgth	Bdth	Lgth	Bdth	Lgth	Bdth	Lgth	Bdth
O. crassidens .	6·6	4·0	8·7	7·2	12·0	9·2	14·0	10·7	11·5	9·0
O. afer . .	5·6	3·0	7·4	5·6	11·4	8·0	12·4	9·0	9·9	7·5
*O. gaudryi** .	5·5	3·0	8·5	5·5	12·5	7·5	14·0	8·5	10·0	6·5
O. depéreti .	—	—	6·8	5·8	11·6	7·8	12·3	8·2	10·3	7·2
O. browni .	—	—	—	—	—	—	7·7	5·3	4·7	4·7
O. pilgrimi .	—	—	—	—	—	—	—	—	—	—
LOWER TEETH										
O. crassidens .	—	—	8·0	5·5	13·7	9·5	15·0	11·2	12·2	9·7
O. afer . .	—	—	6·8	3·7	11·8	7·9	12·9	9·7	10·6	8·3
O. gaudryi .	—	—	8·0	5·0	12·0	7·5	13·0	8·5	11·0	7·0
O. depéreti .	—	—	—	—	—	—	—	—	—	—
O. browni .	—	—	—	—	—	—	—	—	—	—
O. pilgrimi .	—	—	—	—	—	—	10·5	7·0	—	—

* Colbert (1941) gives measurements of eleven examples of *O. gaudryi*. For the purpose of this table, the specimen with the greatest length has been selected in each case.

REFERENCES

ANTHONY, R. 1934. La dentition de l'Oryctérope. *Ann. Sci. Nat., Zool.*, Paris (10) **17**: 289–322, 19 figs.

CLARK, W. E. LE GROS & LEAKEY, L. S. B. 1951. *Fossil Mammals of Africa*, **1**. *The Miocene Hominoidea of East Africa*. v + 117 pp., 9 pls. Brit. Mus. (Nat. Hist.), London.

COLBERT, E. H. 1933. The presence of Tubulidentates in the Middle Siwalik beds of India. *Amer. Mus. Novit.*, New York, **604**: 1–10, 8 figs.

—— 1941. A study of *Orycteropus gaudryi* from the Island of Samos. *Bull. Amer. Mus. Nat. Hist.*, New York, **78**: 305–351, 25 figs.

DUVERNOY, G. L. 1853. Mémoire sur les Oryctéropes du Cap, du Nil Blanc ou d'Abyssinie, et du Sénégal. *Ann. Sci. Nat. Zool.*, Paris (3) **19**: 181–203, pls. 9, 10.

FILHOL, M. H. 1894. Observations concernant quelques mammifères fossiles nouveaux du Quercy. *Ann. Sci. Nat., Zool.*, Paris (7) **16**: 129–150, 21 figs.

HELBING, H. 1933. Ein Orycteropus-Fund aus dem Unteren Pliocaen des Roussillon. *Ecl. geol. Helv.*, Lausanne, **26**: 256–267.

HEUVELMANS, B. 1939. Le Problème de la dentition de l'Oryctérope. *Bull. Mus. Roy. Hist. Nat. Belge*, Bruxelles, **15**, 40: 1–30, 16 figs.

HOPWOOD, A. T. 1954. Notes on the Recent and Fossil Mammalian faunas of Africa. *Proc. Linn. Soc. London*, **165**: 46–49.

JEPSEN, G. L. 1932. *Tubulodon taylori*, a Wind River Eocene tubulidentate from Wyoming. *Proc. Amer. Phil. Soc.*, Philadelphia, **71**, 5: 255–274, pl. 1.

LÖNNBERG, E. 1906. On a new *Orycteropus* from Northern Congo and some remarks on the dentition of the Tubulidentata. *Ark. Zool.*, Uppsala, **3**, 3: 1–35.

OWEN, R. 1840–45. *Odontography ; a treatise on the comparative anatomy of teeth*. xix + lxxiv + 655 pp., atlas 168 pls. London.

THOMAS, OLDFIELD. 1890. A milk dentition in *Orycteropus*. *Proc. Roy. Soc. London*, **47**: 246–248, pl. 8.

EXPLANATION OF PLATES

PLATE 1

Myorycteropus africanus

F~IG~. 1.   Left maxilla of holotype (labial).   Natural size.

F~IG~. 2.   Left maxilla of holotype (occlusal).   Natural size.

F~IG~. 3.   Left mandibular ramus of holotype (labial).   Natural size.

F~IG~. 4.   Left mandibular ramus of holotype (occlusal).   Natural size.

F~IG~. 5.   Photomicrograph: TS of anterior part of left upper Pm^4 of holotype. $\times 36$ diam.

F~IG~. 6.   Left upper M^2 of holotype (occlusal). $\times 6\cdot 5$ diam.

F~IG~. 7.   Left lower M_2 of holotype (occlusal). $\times 5$ diam.

F~IG~. 8.   Photomicrograph: TS of fragment of mandible No. 23 '48, showing Pm_4 and part of M_1. $\times 15$ diam.

NB.—(1) In Fig. 6 it can be seen that the columns are clearly visible on the surface of the crown, even without polishing.

(2) In Fig. 7 the damaged area of the lower M_2 is visible in the postero-internal region of the anterior lobe, and the differentiation of the peripheral columns can be distinguished.

Brit. Mus. (Nat. Hist.)
Fossil Mammals of Africa, 10

PLATE I

MYORYCTEROPUS AFRICANUS

PLATE 2

Brit. Mus. (Nat. Hist.)
Fossil Mammals of Africa, 10
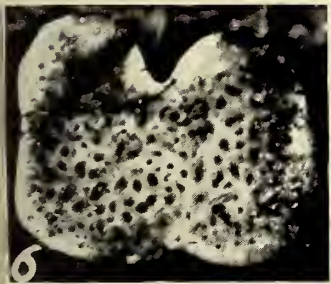
PLATE 2
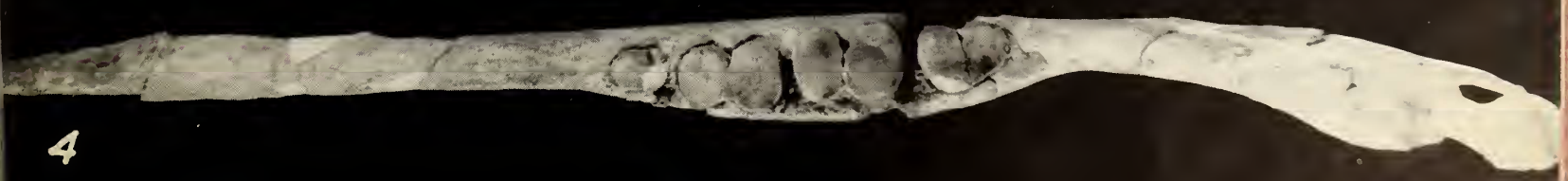

MYORYCTEROPUS AFRICANUS

PLATE 3

5 cms.
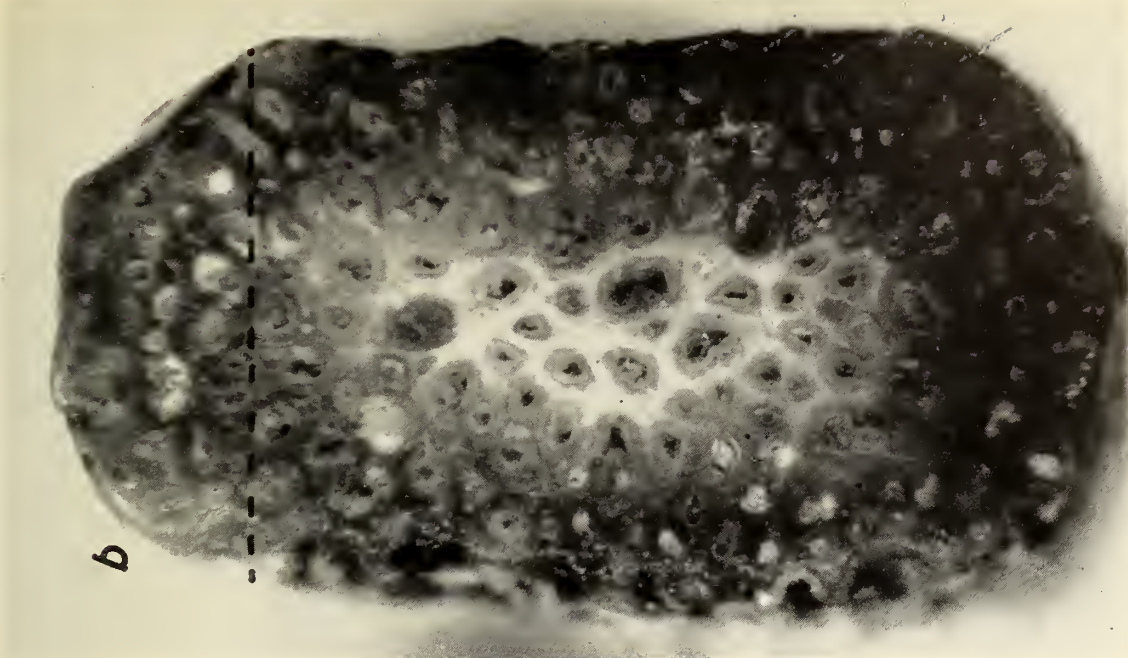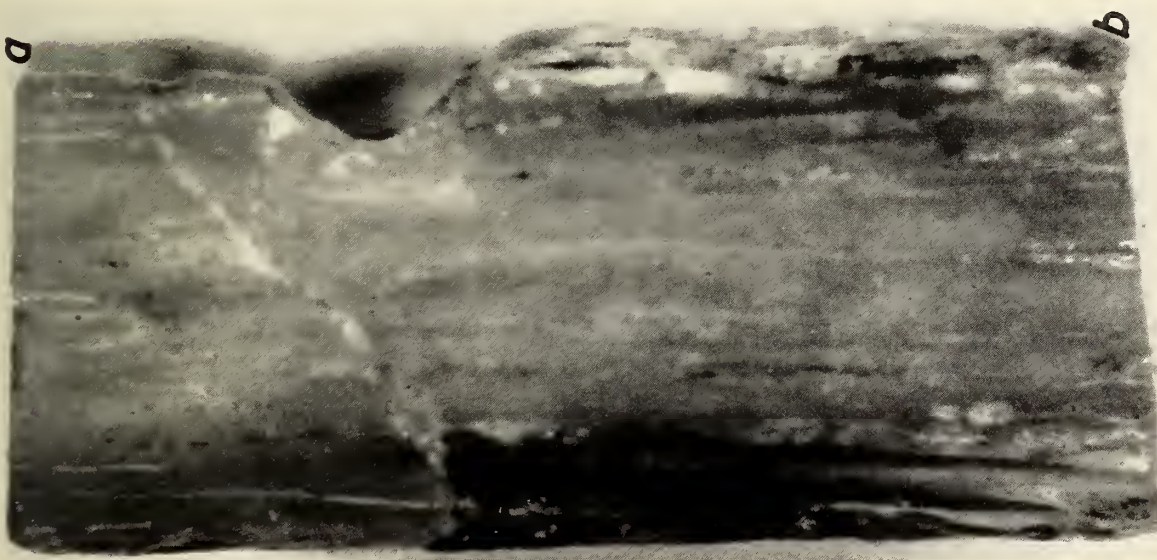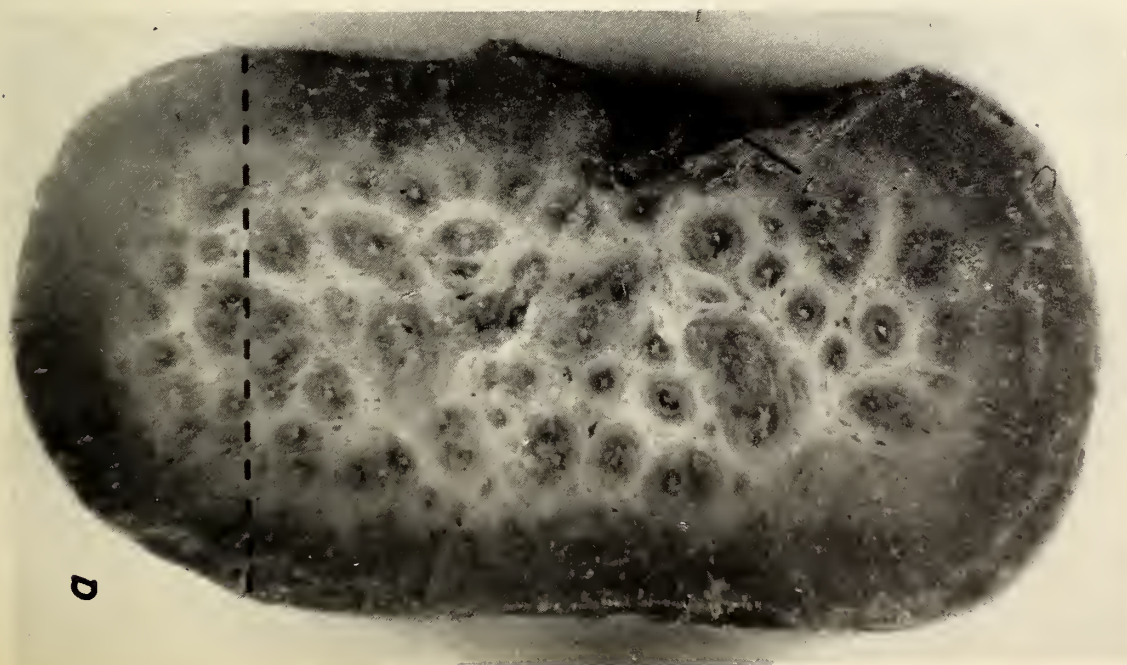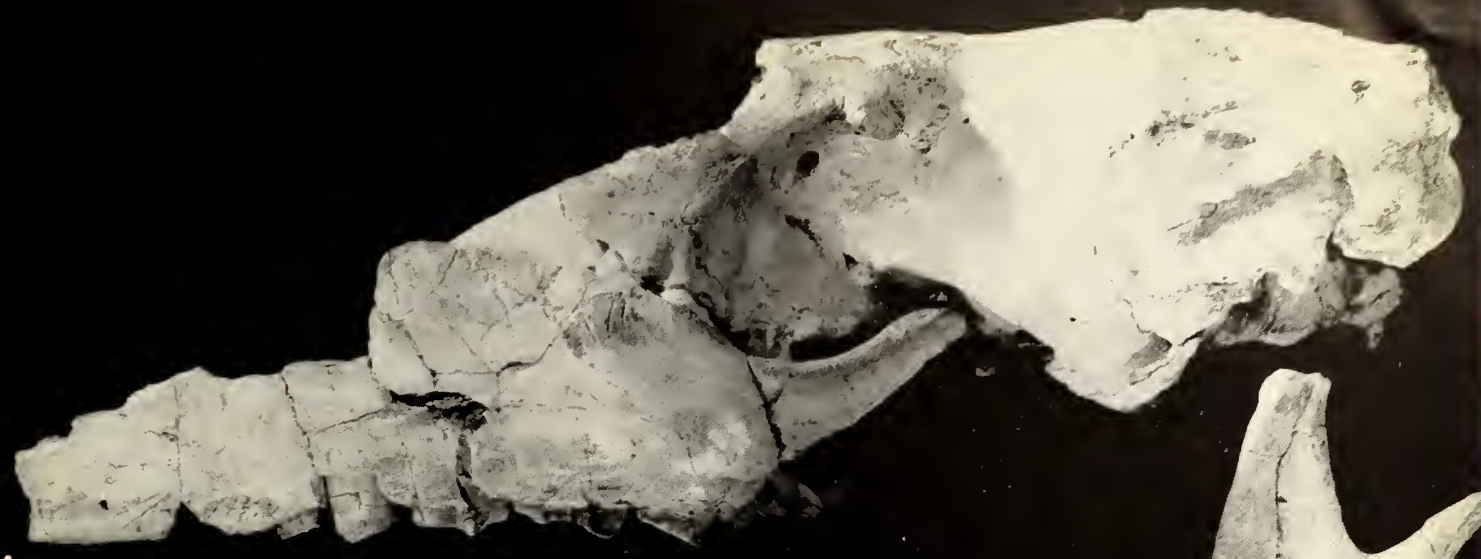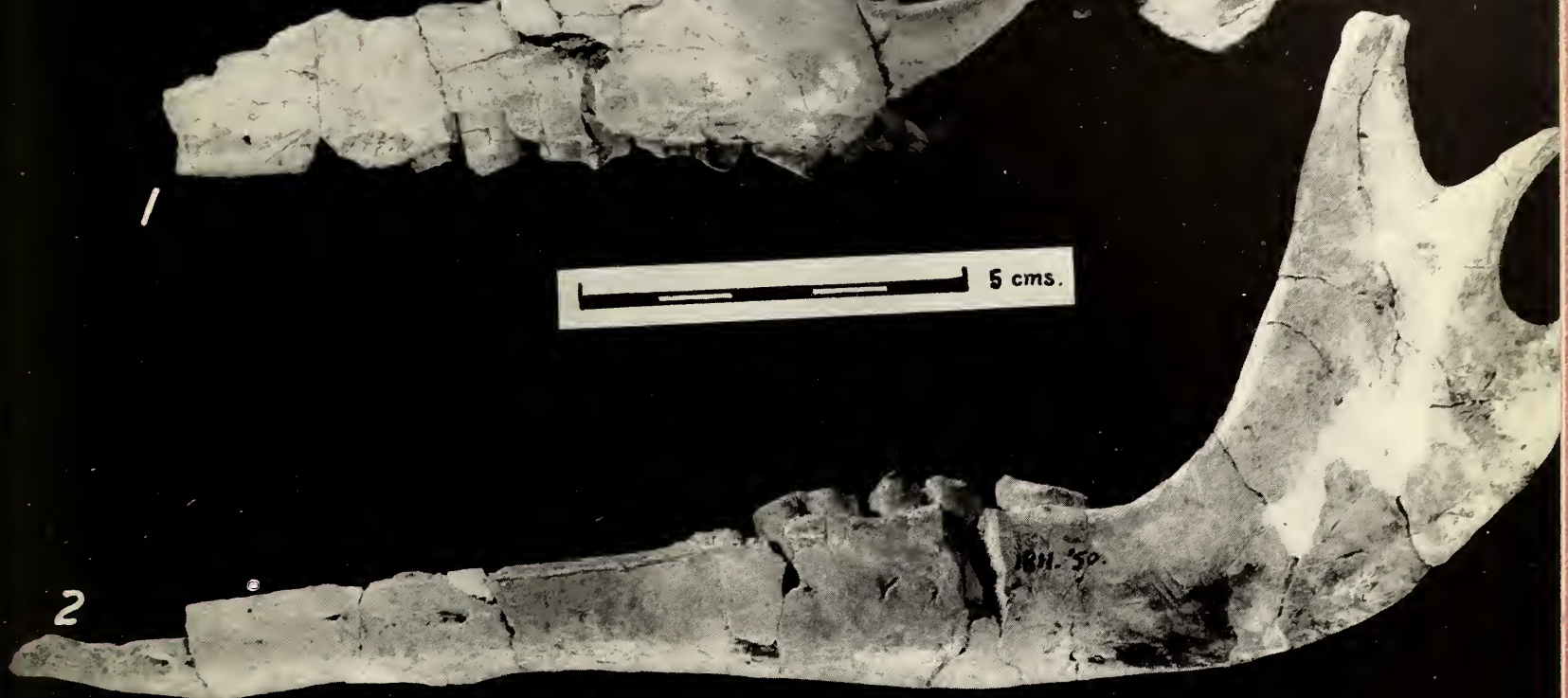
PLATE 4

EXPLANATION OF PLATE 4

Photomicrographs of Tubulidentate teeth

FIG. 1. *Orycteropus afer*.   TS of upper Pm^4 of sub-adult.   × 25 diam.

FIG. 2. *Orycteropus afer*.   TS of upper Pm^4 of old animal.   × 25 diam.

FIG. 3. *Orycteropus afer*.   LS of lower M$_2$.   × 25 diam.

FIG. 4. *Orycteropus crassidens*.   LS of lower M$_2$.   × 30 diam.

FIG. 5. *Orycteropus afer*.   TS of lower M$_2$.   × 25 diam.

FIG. 6. *Orycteropus afer*.   TS of columnar structure.   × 80 diam.

FIG. 7. *Orycteropus crassidens*.   TS of lower M$_2$.   × 25 diam.

NB.—In Figs. 3 & 4 the top of the figure is nearest to the crown.

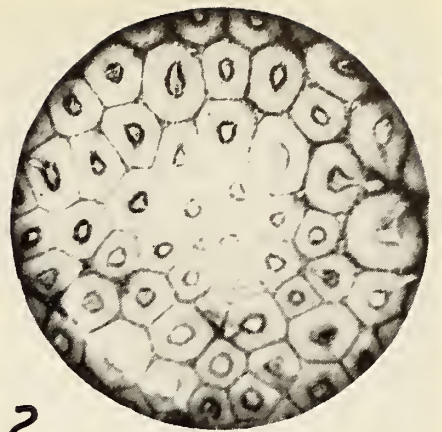In Fig. 3 the columns can be seen entering from the outside.

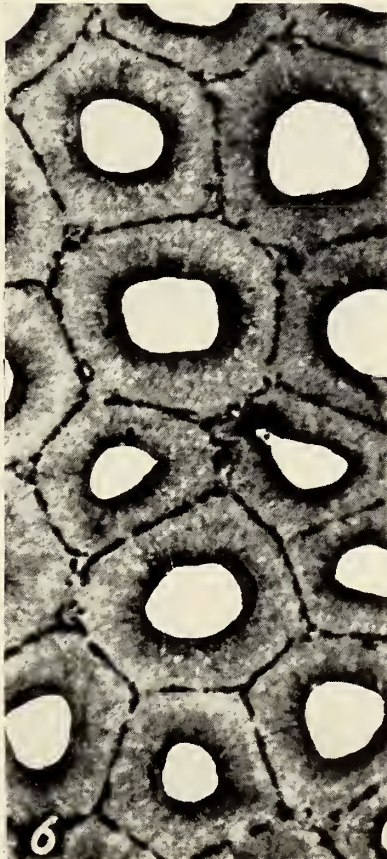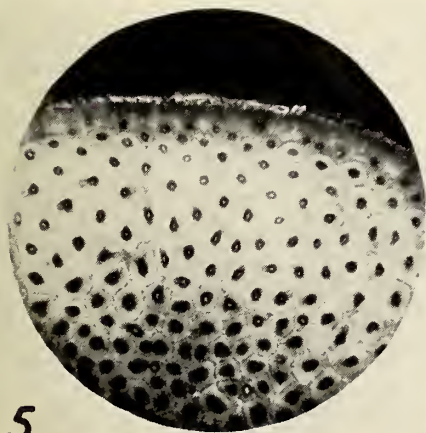Fig. 7 shows some of the peripheral columns enclosed by the surface cementum.
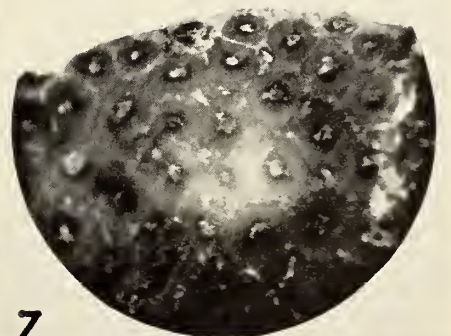
Brit. Mus. (Nat. Hist.)
Fossil Mammals of Africa, 10

PLATE 4
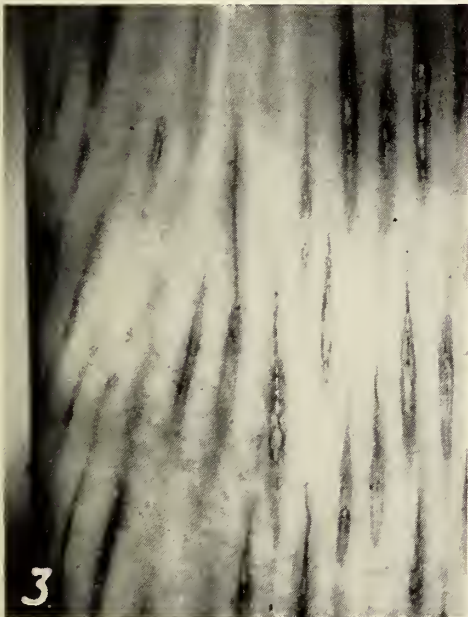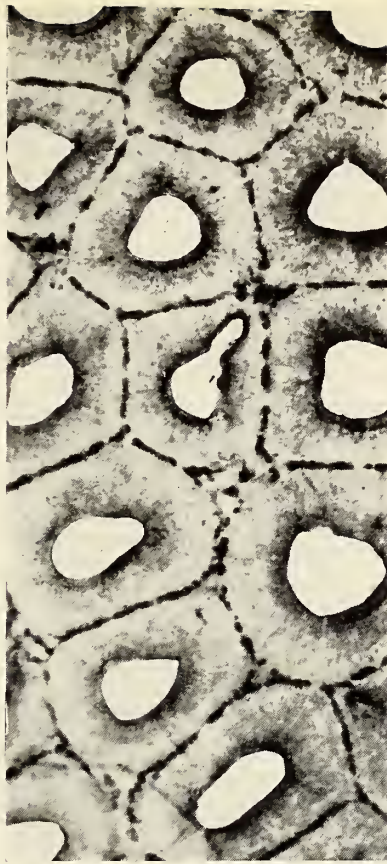
ORYCTEROPUS AFER and O. CRASSIDENS